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FROM the highlands of central Mexico across the entire United States and northward into Canada extends the great mid-continental prairie. On the east it is in contact with the deciduous forest. From this central mass the prairie extends westward beyond the Rocky Mountains across Wyoming into eastern Utah, and southwestward through northern New Mexico into northern Arizona. The Palouse Grasslands occurred in eastern Oregon and Washington, and other parts of the far Northwest. The Pacific Prairie was found in the Great Valley of California, and the Desert Plains Grassland still occupies much of southern Arizona and New Mexico and southwestern Texas. Together they constitute the Grassland or Prairie Formation, which is the most extensive and most varied of all the natural units of vegetation of the North American continent. In fact, native grassland formerly covered 38 per cent of the entire land surface of the United States.

Throughout the entire Prairie Formation the climate is more favorable to grasses than to trees or shrubs or, indeed, to any other type of vegetation. But within the vast range of grassland climate, marked differences exist in degrees of favorableness for growth. These are illustrated especially by differences in precipitation and relative rates of evaporation. Temperature and length of growing season are of less importance, for all the grasslands seem to lie well within summer temperature limits favorable to growth of the grass life-form. Since rainfall decreases and evaporation increases from east to west in the great mid-continental area, there have resulted several different kinds or associations of prairie, each limited in extent by a distinctly different minor grassland climate.

This vast prairie is in summer a sea of waving grasses: Except

for its grandeur of expanse, and the wealth of splendid flowers, the prairie appears almost monotonous in the general uniformity of its cover. The absence of trees, the paucity of shrubs, the dominance of grasses, and a characteristic drought-enduring flora constitute its main features.

The recognition of the communities of which prairie is composed, the wonderful manner in which they are organized, the leading role played by dominant species, and the close adjustment of the various species to their physical environment and to each other have only recently been clearly comprehended, even by students of grassland.

In correlation with the amount of precipitation, grasses fall rather naturally into three groups: tall grasses such as big bluestem and slough grass which grow six to eight or more feet tall; mid grasses, like little bluestem and needle grass which are two to four feet in height; and short grasses as illustrated by buffalo grass and blue grama, whose heights range between 0.5 and 1.5 feet. Tall grasses occur in the wetter, eastern portions of the grassland where precipitation is thirty-five inches or more. They are also found westward on lowlands along streams where precipitation is supplemented by water running down the slopes, and in the general prairie area on sandhills where no water is lost by runoff and little is wasted by direct evaporation through the surface mulch of dry sand. Conversely, short grasses occur mostly in areas of low precipitation such as the Desert Plains Grassland of the far Southwest, and in the more arid portions of the main mass of grassland west of the hundredth meridian of longitude under a precipitation of fourteen to twenty-three inches. Under intermediate conditions, as over the uplands of Iowa and eastern Nebraska, mid grasses thrive. They intermingle with tall grasses on lower slopes but are shaded out by them in low wet soil. On the upland, in turn, short grasses are rarely found except on the steepest and driest hilltops, since they cannot endure the shade of closely spaced mid grasses. This results in a great body of mid grasses, commonly called True Prairie, extending eastward from Nebraska across Iowa and Illinois, but with Tall Grass Prairie not only on its eastern border but also dissecting it along the flood

NORTH AMERICAN PRAIRIE

plains of the thousands of streams. The long axis of True Prairie lies north and south, from Canada to southern Oklahoma.

West of a broad transitional area, approximately along the hundredth meridian, precipitation becomes too light, with increased evaporation, to support a continuous stand of mid grasses, and they are more or less widely spaced. The open spaces between have long been claimed by an understory of buffalo grass, blue grama, or other short grasses. The result is a two-story prairie of short grass and mid grass intermixed, eight-inch blue grama for example under two-foot western wheat grass. This, the most massive association of all and the one that extends westward beyond the Rockies, is appropriately designated Mixed Prairie. Southward it reaches far into western Texas; on the north it stretches half way across Saskatchewan. This extensive Mixed Prairie association has been grazed so intensively that in most places over its drier western part the mid grasses have all but disappeared. Short grasses have increased greatly and such areas have been designated short-grass plains. Climatically they are mixed prairie. Only in the arid Southwest does the extremely low precipitation, coupled with a remarkably high rate of evaporation, exclude mid grass. The Desert Plains association is truly one of short grasses.

Prairie everywhere owes its character to the most abundant and important grasses. These are called dominants, since they largely control the abundance, vigor of growth, and often the very existence of other species. This control is exerted through their effects upon the water supply, light, and other factors of the environment. Most of the dominants are bunch-formers although some propagate by rhizomes, and rarely by stolons, to form a dense sod. Indeed, when one learns to recognize eight or ten dominants in any prairie association and becomes familiar with their life habits and the places in which they thrive, he is well on the way toward an understanding of grassland. This is true despite the fact that in True Prairie, for example, there are fifty or more other important but subdominant grasses and numerous other species.

The various groupings or types of grassland even within a single

square mile are delimited by the presence in abundance of a single dominant or two or three dominant grasses on somewhat equal terms. Even the layman recognizes and understands what is meant by bluestem, slough grass, needle grass, or wheat grass prairie. In fact, the entire True Prairie from Minnesota to Missouri and from Kansas to Dakota has been found to contain in the main only six communities or types, three on lowland and three on upland.

In wet, poorly drained or waterlogged soil (in sloughs) occurs the tall, coarse slough grass, often in practically pure stands. Where the soil is wet in spring but later well drained and aerated, big bluestem holds forth in growth so tall and stands so dense that the herds of cattle of the early settlers were lost to view and could be found in evening only by the tinkling of the cowbell or the waving of the tops of the nine-foot bluestem or Indian grass, a phenomenon best observed from horseback. This was the famous bluestem corn land. But so thick and tough were the rhizomes and roots that the soil was always broken by preference only after grazing or repeated mowing had weakened the hold of the bluestem.

Between these types lies land too dry for good development of slough grass and too poorly aerated for big bluestem. Here thrives a community of tall switch grass or nodding wild rye or an intermixture of the two dominants. As in the other lowland types, the light is so greatly reduced by the tall, dense stands of the dominants (often only 1 per cent reaches the soil) that most other species are excluded. Of the three lowland types, however, big bluestem is by far the most extensive.

On upland, little bluestem usually dominates all but the driest slopes and hilltops. Here occurs needle grass, ripening in June not unlike a field of grain, or dense, nearly pure stands of prairie dropseed.

Grasses are well adapted to withstand the grazing that has been imposed upon them through thousands of years by herds of bison, elk, and other native animals, followed by the settlers' cattle. Near the base of the leaf there is a transverse intercalary zone of growth. Hence if the major portion of the leaf is cut or bitten off

NORTH AMERICAN PRAIRIE

the part can readily be replaced; that is, the leaf can grow from the base until it reaches or surpasses its former size. Portions of stems of grasses as well as the leaves are also removed in grazing. Growth then takes place from buds produced in the axils of sheathing bases of the leaves at the lower end of the stems. Yet grasslands contain other kinds of plants — herbs that do not have the grass life-form. These are designated as forbs.

Forbs have accommodated themselves to the presence of grasses, as is shown by their seasonal activities and differences in height. The groups or societies of forbs and the degree of development of the grasses lend to each season a distinctly different appearance or aspect. The prairie presents four aspects, besides the more somber one of winter. The orderly succession of changes in the conspicuous features of the landscape proceeds with marked regularity.

In the earliest aspect, prevernal bloomers in the central prairie area appear in the warmer situations late in March or early in April. Among the most important are prairie cat's-foot, pasque flower, dog's-tooth violet, windflower, and fennel-leaved parsley. Needle grass, June grass, and nodding wild rye, all of northern extraction, are the only dominant grasses that have made considerable growth, but this is exceeded by the rapid development of bluegrass.

Late April introduces the vernal or spring aspect. The drab tone of winter is replaced by the greenish tinge of the new growth of grasses. The bluestems, of southern origin, appear about the middle of April, but on low ground and north slopes the colors of the dried vegetation of the preceding fall are not entirely obscured until the first week of May. This period initiates rapid growth of plants of summer and autumn as well as those of spring. In the ravines and moist soil the tall-growing, sawtooth sunflower, rosinweeds, tall goldenrod, and other late bloomers far outstrip the grasses in rate of growth. Strawberries, violet wood-sorrel, and prairie violet develop both foliage and flowers before the light is too much obscured by the rapidly growing grasses. The new shoots of blazing stars, goldenrods, sunflowers, and sage add tone to the landscape. In spring the prairies pulse with life.

From the background of green show forth the gems of nature, manifold in variety, radiant in beauty, endless in recurrence — the societies of the vernal aspect. Among these are found blue-eyed grass, yellow star grass, puccoons, old-man-of-the-Platte, wild onions, vetches, false indigo, spiderworts, and many others, all enhancing the beauty of prairie in spring. The yellow of the golden parsnip, the bright pink or purple of the prairie phlox, the white masses of flowers of New Jersey tea, and the buffalo bean with its abundance of violet-purple flowers were all familiar sights to the pioneers of the Midwest.

The estival or summer aspect begins during the last week of May. By this time bluegrass has blossomed, the spikes of June grass are beginning to open, and needle grass is often in full bloom. The bluestems and other dominant grasses now cover the uplands with a deep foliage of green, and on the lowlands a height of twelve to eighteen inches has been attained. Many spring flowers are gone. Although certain vernal species continue to bloom, there is a distinct transition from spring to summer. The landscape is rapidly becoming redecorated with extensive societies of daisies, legumes, and the rose. Milfoil, daisy fleabane, pentstemons, larkspurs, wild flax, primroses, and purple cone-flower adorn the hillsides. The stately plants and showy flowers of several species of wild lily add further variety to nature's varicolored garden.

Myriads of flowers now contribute to the great wealth of mid-summer beauty. Among the most distinctive and widely spread societies of upland is that of prairie shoestring. Even before the abundant dark purple or indigo flowers begin to appear in June, the leaden-colored leaves give tone to the prairie. Profuse blossoming continues several weeks. The white and purple prairie clover, black-eyed Susan, tick trefoil, wild licorice, wild bergamot, and rosinweeds adorn the rolling hills and lowlands. The patterns are endlessly variable in detail. Each week new elements appear and old ones gradually decline as the season advances. The blooming of the sunflower and the yellowing of the inflorescences of the goldenrod portend the coming of fall. Again the scenes are shifted as the summer aspect gives way to the autumnal one.

NORTH AMERICAN PRAIRIE

About the middle of July the prairie begins to change gradually in appearance. The graceful flower stalks and flowers of side-oats grama, which have been developing slowly, now appear in abundance for the first time. The spikes of nodding wild rye are nearing their height of blossoming. Soon the panicles of the switch grass on low ground begin to unfold, and isolated stalks of the blue-stems overtop here and there the vegetative growth which is now nearly complete. The deep cover of grasses, although still green and vigorous, has passed from a stage of active development to one of approaching fruition and maturity.

Most of the estival plants have finished blooming; others are distinctly on the wane; but many continue into the autumnal aspect, at least for a time. Now the yellow and gold of the sunflower and rough oxeye intermingle with the purple of the blazing stars. Many species of goldenrods occur, sometimes in great masses, and all add much beauty to the autumnal landscape. Various rosinweeds dot the prairie where moisture is plentiful. Pleasing variety is added to the wealth of autumnal colors by the grayish white flowers of the false prairie boneset, the gray color of the prairie sage, and the black fruiting heads of lespedeza. Ironweeds, gentians, evening primroses, and many others are found. Numerous asters blossom from August until late fall, their colors varying from white or lavender to blue or purple.

During September and late fall, the great fields of fruiting grasses are beautiful to behold. On low ground scores of the forked inflorescences of big bluestem may occur on every square yard. The golden panicles of Indian grass glisten in the sun. The dried heads of nodding wild rye stand thickly in the ravines, while on uplands the open panicles of prairie dropseed are held aloft above the level of the foliage. About the first week in September many prairie grasses begin to lose their green color and slowly take on the red and bronze and golden tints of autumn. These gradually deepen until the landscape presents a color scheme rivaled in beauty and delicacy of painting only by the autumnal coloration of the great deciduous forests. Late October or November witnesses the waning and finally the death of the aerial parts of the forbs and grasses. Life in the prairie retreats underground.

As a result of natural deterioration, augmented by the work of the wind and assisted by the weight of ice and snow, the once great cover of standing vegetation gradually returns to the surface of mother earth. Here it forms a protecting blanket for the living parts within and beneath the surface of the soil. But the prairie is still a living thing — though underground and dormant — awaiting only another summer to build anew the parts above the soil.

Plants are extremely crowded in their prairie home. Competition for light is often severe. Many forbs of early spring always remain near the surface of the soil. They make a rapid growth, flower and produce seed early, and thus complete the important work of the season before they are overshadowed by the grasses. Many species of late spring are likewise of low stature. But some, such as phlox and golden meadow parsnip, may exceed the grasses in height for a time. By midsummer nearly all are submerged to the general grass-level.

Plants which blossom during midsummer or fall have likewise started an early vigorous development. They grow rapidly. Week by week during early summer the struggle for light becomes more and more severe. Species of the summer aspect attain a moderate height, but autumnal blooming plants continue to elongate until they are mostly far above the grasses. Not one is found in the understory. Except for the gentian, all are conspicuous at or above the general grass-level and many reach a height of four to six feet or more.

Within the prairie cover one finds the conditions of life severe. Though the soil is rich and deep, water is frequently scarce and the plants sharing it are legion. Deficiency of water usually occurs when the air too is driest, the temperature high, and the prairie swept by desiccating winds.

The problem of an adequate water supply has been met by the development of deeply penetrating, usually widely branching, and thoroughly efficient root systems. The perennial life habitat is exhibited by all but a few of the prairie species. Hence a good absorbing system, once established, may be used throughout a long span of years. Moreover, the roots and other underground

NORTH AMERICAN PRAIRIE

parts are storehouses of food during the long period of winter dormancy and account for the rapid growth of the plants following their early awakening in spring.

Layering in prairie also occurs in the soil. Roots of different species do not all draw upon the same soil level for their supplies of water and nutrients. Indeed the root habit is so fixed in this respect that the various species may be grouped according to the layer or layers of soil occupied by them. A small percentage of plants extend their roots only about 1.5 feet deep; moderately deeply rooted plants attain a depth of four to five feet. But about 65 per cent of prairie species extend their roots beyond five feet, maximum depths of eighteen to twenty-four feet sometimes being attained. Indeed, the bulk of the prairie is below and not above the surface of the soil.

Thus, the plan of life in the prairie is very diverse. So many species can exist together only by sharing the soil at different levels, by obtaining light at different heights, by making maximum demands for water and soil nutrients at different seasons of the year, by fitting into the niches unoccupied by other species, and by profiting by the incidental benefits afforded by the community of which they are a part.

The great stability of the prairie denotes a high degree of equilibrium between the vegetation and its habitat under the control of the existing climate. Large tracts of prairie, after ninety or more years of settlement, remain practically uninvaded by weeds except to the extent that trails or roads have been made through them or soil has been washed into the ravines from adjacent fields. With rare exceptions, they remain free from weeds, although surrounded for years by weedy fields and pastures.

Stability is increased by the long life of many prairie plants. The dominant bunch grasses, once established, retain their vitality for many years. The life span of certain forbs may extend over several decades. The prairie itself is an intricately constructed community. The climax vegetation is the outcome of thousands of years of sorting of species and adaptations to soil and climate. In fact it is more than this, for the vegetation has had no small part in determining the physical, chemical, and biological prop-

erties of the soil. Prairie soil and prairie climate are in a sense an expression of one and the same thing. Indeed, the development of the soil and a parallel development of the plant cover have gone hand in hand from the beginning of rock weathering to the production of mature soil covered with climax prairie.

The constructional processes of soil development are due largely to the incorporation of plant parts and microorganisms among the mineral particles. Upon the fall of leaves and stems the organic matter of the plant, which has resulted from synthetic activity, is incorporated into the soil. These residues of grassland vegetation have returned more to the soil than the green plants have absorbed from it. Throughout their lives plants have synthesized many organic substances — sugars, starches, celluloses, fats, and proteins. Most of these materials return to the soil when the plant dies. This added organic matter produced by vegetation introduces a fundamental change. The substrate is no longer the former one of mineral matter alone, but now contains stored energy in the form of organic material, and a microflora of bacteria, fungi, and other organisms.

The amount of living organic materials in prairie soils is very great, often three to four tons an acre in a surface of four inches. Thus, when the farmer mows his prairie in fall and the yield is two to three tons of air-dry hay per acre, he is leaving a still larger amount of living plant material in the surface four inches of the meadow. Here roots are so abundant and their branches so very numerous and fine that their total length within a square yard of soil even to the four-inch depth is often twenty or more miles.

A reaction of major importance of the prairie cover occurs in breaking the force of beating rains. Even torrential downpours, so characteristic of prairie climate, reach the soil with the velocity of the raindrops much decreased. Not only is the force of the impact reduced, but the surface soil is not churned into a muddy suspension as is bare soil. The fine particles of soil remain in place and do not clog the pores as the water enters the soil. That the pores remain open is a chief reason for the great absorptive power of prairie soil. Runoff water in prairie is usually slight unless rains are heavy. The water that does run off is clear, since the soil

NORTH AMERICAN PRAIRIE

is protected by litter and leaf mold and held firmly in place by the bases of the plants and their widely and deeply spreading root systems. Nor does erosion by wind occur where there is a natural cover of grass.

Grassland soils through untold centuries have been thoroughly protected by the unbroken mantle of prairie vegetation. The vegetation and soil are closely related, intimately mixed, and highly interdependent upon each other and upon the climate. Hence prairie is much more than land covered with grass. It is a slowly evolved, highly complex organic entity, centuries old. It approaches the eternal. Once destroyed, it can never be replaced by man.

University of Nebraska, January, 1944