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FLOOD PLAIN VEGETATION OF THE CENTRAL MISSOURI VALLEY AND CONTACTS OF WOODLAND WITH PRAIRIE

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INTRODUCTION

The Missouri River, like some of its great tributaries, rises high in the Rocky Mountains. With thousands of tributary streams it drains the water from plains and prairie to form a mighty river with a flood plain many miles wide. It has made a bluffrimmed depression and numerous tributaries and their branches have cut canyons below the general level of the wind-swept grasslands. Its main tributaries from the west-the Niobrara, Elkhorn, Platte, and Big Blue-flow east or southeastward. The Big Sioux River bordering Iowa, enters the Missouri from the north, and large tributaries in Iowa-the Little Sioux, Boyer, Nishnabotna, Tarkio and Nodaway-flow more southward than westward (Fig. 1). The Missouri River separates southeastern South Dakota, Iowa, and a part of Missouri from Nebraska. So profoundly has this river modified the effects of the general grassland climate that in many places prairie has given way to woodland and forest.

Several distinct forest communities along the river in southeastern Nebraska and adjacent parts of Kansas, Missouri, and Iowa extend for short distances over the uplands, but farther along the major streams. Most of the trees and shrubs of this forest are near the extreme western limit of their range. The extreme outposts of the forest are represented by relatively few species of trees and shrubs along the creeks and sheltered ravines which more or less dissect the hilly and rolling portions of the prairie.

With these the grassland had immediate contact over many thousands of miles.

The several belts of forest communities on the river bluffs and adjacent hills are, beginning with the most mesic, red oak-linden (*Quercus borealis maxima* and *Tilia americana*), black oak-shellbark hickory (*Quercus velutina* and *Carya ovata*), and bur oak-bitternut hickory (*Quercus macrocarpa* and *Carya cordiformis*).

The bur oak community is usually but not always bordered by a more or less continuous community of shrubs which separate it from prairie. Northward beyond the mouth of the Platte the more mesic forest communities almost disappear. There is a decrease in the general area occupied by woody vegetation, decrease in number of species, dwarfing in size of individuals, and trees are confined to the more favorable sites. Conversely, the area covered by shrubs greatly increases.

Tongues of woodland follow up the stream courses into Iowa northeastward to the Missouri-Mississippi divide, and far into Nebraska and northern Kansas westward. Such belts of timber vary from a few yards in width at the stream sources in grassland to 0.5 mi or more along their lower limits where they merge insensibly into the main body of timber on the Missouri River bluffs and along the valleys.

The area of this study is approximately 50,000 sq mi. It includes the portion of the Missouri Valley in western Iowa, eastern Nebraska and parts of the 3 adjoining states. Forested areas in the Missouri

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FIG. 1. Central part of the Missouri River and its tributaries.

Valley drainage of western Iowa are less abundant than those west of the river. In southeastern Nebraska the average width of the general potential forest area is, according to Aikman (1929), about 15 mi; in the vicinity of Omaha it is about 5, but in northeastern Nebraska 2 mi or less.

The general surface of the land is not greatly diversified. Much nearly level land occurs, but rolling to hilly country predominates. Drainage is from an elevation of approximately 1,250 ft near the Nebraska-Dakota line to 850 ft in the southeast (Nebraska-Kansas boundary).

The soil has developed from transported material. Loess formed a mantle over glacial deposits in nearly all of the area, but in parts of it the covering of loess has been eroded away. Chief exception occurs in a relatively small part of northern Nebraska and southeastern South Dakota where outwash plains soil of gravel, sand, and finer materials are intermixed. There are extensive alluvial flood plains, 1 to 17 mi wide, along the larger rivers. In general, the soils are deep, fertile, fine-textured loams of high water-holding capacity and usually circumneutral in reaction. They all have great depth and are usually moist but not wet throughout.

Mean annual precipitation varies from about 34 in. in the southeast to only 23 in. in the northwest. There is usually a single period of heavy rainfall during the growing season. In the southeast this includes 5 spring and summer months but in the northwest only about 2.

Forest communities rapidly disappear along streams outward from the Missouri River, and the

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typical condition is a mingling of upland trees with those of the flood plain. Farther from the great river, trees are mostly confined to the banks of larger streams and to broad shallow ravines tributary to them, or to the vicinity of springs. Some are found in the shelter of steep protecting bluffs. In the driest prairies trees occur naturally, if at all, only as small groups or as individuals in the most protected places.

The beginnings of woody vegetation at the headwaters of streams and its increase in kinds and number of species, as the stream provides a proper environment, will first be described. Then the results will be given of an extensive survey of the various types of vegetation which occupy the flood plains of the larger rivers.

Names of grasses are according to Hitchcock & Chase (1950) revised Manual of the Grasses of the United States. Other scientific names follow Gleason's (1952) New Britton & Brown Illustrated Flora.

ORIGIN AND DEVELOPMENT OF STREAMS AND THEIR WOODY VEGETATION

No land area is perfectly flat or perfectly smooth and much land is rolling or hilly. Although runoff water may at first form a thin sheet flowing evenly downward, it is concentrated by converging slopes into the shortest and steepest downward route. It is soon reinforced by water from runoff, seeps and springs from other hillsides and a definite stream is formed.

The headwaters of many streams have been investigated where they originated in unbroken prairie sod. At first the course is marked by an increase in abundance and stature of the more mesic grasses and forbs, especially big bluestem (*Andropogon gerardi*), when compared with those on adjoining slopes. Soon an intermittent stream, dry except after heavy showers, begins to cut into the sod to form a channel. As the channel deepens and widens along the first few miles of its course it presents a habitat where wind-blown seeds of willow and cottonwood may germinate and the seedlings develop. This may occur as soon as the soil is bared; then all along the stream, as isolated individuals or intermittent clumps, Salix amygdaloides, S. migra or Populus sargentii appear.

A few miles farther down the valley one may observe a slow, meandering stream, nearly dry in late summer but with banks 2-3 ft high, wending its way through wet meadow, or a spring-fed one which has ceased to be intermittent. The latter, joined by other streams, has cut its banks 10 ft wide or more and 6-8 ft deep. On both streams wind-protected, sloping banks were favorable sites for certain shrubs. Chief among these were coralberry (Symphoricarpos orbiculatus), wolfberry (S. occidentalis), elder (Sambucus canadensis) and indigobush (Amorpha fruti-Present in smaller numbers were smooth cosa). sumac (Rhus glabra), wild gooseberry (Ribes missouriense), frost grape (Vitis vulpina) and bittersweet (Celastrus scandens). Willows, 8-15 in. in diameter, and cottonwoods, a few 3-4 ft thick, were

much older and larger than those upstream. Green ash (Fraxinus pennsylvanica) and boxelder (Acer *negundo*) were sometimes represented by a few small trees. Farther downstream an increasingly large number of both trees and shrubs occurred as well as a beginning of their separation into different habitats. Fine large trees of red or slippery elm (Ulmus rubra) and white or American elm (U. americana) were most abundant on the banks. Flood plain species were boxelder, green ash, hackberry (Celtis occidentalis), honey locust (Gleditsia triacanthos), wild black cherry (Prunus serotina) and black walnut (Juglans nigra). Some of these, of course, grew near or among the elms as well as on the base of the slope. A scattered growth of young bur oak, usually with diameters of 5 in. or less, grew on protected north-facing slopes and sides of lateral ravines.

Aside from shrubs and vines found upstream, which occurred much more abundantly here, several other species had migrated upward from the Missouri River. These were roughleaf dogwood (*Cornus drummondi*), black raspberry (*Rubus occidentalis*), burning bush (*Euonymus atropurpureus*), green brier (*Smilax hispida*), poison ivy (*Rhus radicans*), virginia creeper (*Parthenocissus quinquefolia*), buckthorn (*Rhamnus lanceolatus*) and virgin's bower (*Clematis virginiana*). Most of these were scattered widely over the flood plain.

Continued study of the beginnings of vegetation along streams over this central prairie region, along branches of the Nodaway, Tarkio, Boyer, Elkhorn, and other rivers confirmed the general sequence described. Pioneer trees at the stream sources are those with light, wind-blown seeds such as cottonwood and willows. They usually appear soon after the sod is weakened by erosion. After a suitable habitat is available other species with wind-blown seeds occur. such as boxelder, elms and ash. The pioneer shrubs and vines-elder, coralberry, bittersweet, grape and others-have showy, edible fruits carried by birds. This early stage in woodland development is represented for considerable distances along nearly all small tributaries. It is especially pronounced in the western part of the area as well as northward, along the tributaries of such rivers as the Elkhorn and Big and Little Blue which extend far into the plains. When a stream develops a flood plain with wide protecting banks, large fruits such as walnut, bur oak, hickory, hazel, and others are carried up stream by various animals, especially timber squirrels. Thus, as soon as a suitable habitat is provided in windprotected places along the stream, trees and shrubs may, in the absence of recurring fires, replace the prairie grasses. But on unsheltered and wind-swept banks of prairie streams, especially those far from large rivers, little or no woody vegetation may occur.

Far down most streams in the southeastern part of the area, flood plain forest is separated from bur oak and its border of shrubs by more mesic types of forest, especially red oak and linden.

CONTACTS OF WOODLAND WITH PRAIRIE

Prairie grasses may come in direct contact with trees, especially in the early development of woodland along streams. But usually grassland is replaced by shrubs which extend outward from the edge of the woodland. Of the several species concerned the most important are sumac, rough dogwood, coralberry and hazel (*Corylus americana*). Where shrubs extend into prairie it is by mass invasion. It occurs at a level above most of the prairie grasses and is due to shade cast by the peripheral plants leaning far outward toward the light.

Prairie vegetation is shaded out more or less completely under a closed canopy of sumac or other shrubs. For a time it may be completely replaced by kentucky bluegrass (*Poa pratensis*) which is nearly always present, at least in small amounts, among the other grasses; but ultimately bare soil may prevail.

Shrubs usually extended outward only a few feet or a few yards into prairie. Often their contact with upland prairie was with big bluestem which formed a thin border to the more xeric prairie grasses. On lower slopes a more or less distinct belt of switchgrass (*Panicum virgatum*) with canada wild-rye (*Elymus* canadensis) or sometimes cordgrass (*Spartina peć*tinata) often intervened between bluestem prairie and shrubs.

A typical example of a low prairie-woodland contact follows. Transition from trees to prairie on a south exposure extended over only a few yards. Indeed, along a portion of the eroding creek both soil and trees had been washed away and prairie continued without change to the edge of the vertical bank. Elsewhere at the edge of the prairie the tall grasses were intermixed with an unusual percentage of coarse forbs such as oxeye (Heliopsis helianthoides), sawtooth sunflower (Helianthus grosseserratus), jerusalem artichoke (Helianthus tuberosus) and various species of goldenrod and aster. These first mingled with and then gave way to an intermittent border of roughleaf dogwood, coralberry and poison ivy. Elsewhere switchgrass and canada wild-rye extended to the shade and leaf litter under overhanging branches of the trees. A number of woody and herbaceous vines grew thickly at the forest edge and clambered over shrubs and far up the trees.

The west edge of this prairie, which was best protected from wind and afternoon sun, presented the widest, tallest and most varied fringe of shrubs. Here sumac formed thickets 8-15 ft high; thickets of wild plum (*Prunus americana*) were overrun by virginia creeper; frost grape and other vines were common and dense stands of dogwood, as tall as the sumac, were usual. Tangled vines of black raspberry were plentiful, and over much of the transitional zone poison ivy completely covered the soil with its thick foliage or elimbed up the trees, the lower part of which were all but screened from sight by the mass of shrubs. A wetter part of this wide border was occupied by a thicket of sandbar willow (*Salix interior*).

Not infrequently saline areas occur locally or extend widely over the lower flood plains. Salt Creek and some of its tributaries, for example, receive salty water through springs. Most prairie grasses are intolerant to salt. Hence, the wonderfully well developed bluestem prairies of the upper flood plain were usually separated from the woodland's edge by broad belts of salt grass (*Distichlis stricta*), western wheatgrass (*Agropyron smithii*) and other salt-tolerant grasses. Similar saline areas are common along the Platte, Elkhorn, and Missouri Rivers and hundreds of smaller streams.



FIG. 2. A typical forest of bur oak (Quercus macrocarpa) with undergrowth of various shrubs.

Contacts of upland prairie are usually but not always with bur oak woodland (Fig. 2). This oak often borders dry ravines as well as streams but it is rarely found in wet places. Where oaks occurred in dry ravines between steep hills, the wooded area was usually bounded by prairie right up to the edge of the banks; often shrubs spread outward only a little (Figs. 3, 4). Of the prairie grasses, the taller ones and especially big bluestem seemed to thrive best in the shade of the shrubs and especially under the shade of the branches of bur oak which spread outward near the soil. The half-shade often resulted in a



FIG. 3. Thicket of wild plum (*Prunus americana*) in blossom in spring along a ravine in unbroken prairie. Grasses are kept out by the shade.

border of blue grass on the prairie's edge under the shrubs and oaks. How far the shrubs extend outward is determined by the water supply and exposure to drying winds. Usually it is only a few yards.



FIG. 4. Mowed prairie with bur oak and other trees in a ravine along Oak Creek. Photo in August 1947.

As an eroded dry ravine gradually changes into one with running water, the flood plain trees become grouped nearest the water and the oaks on the upper slopes. Farther downstream where many rivulets joined to form a creek with wide sloping banks, the same general relationships occurred. These are maintained when a flood plain is developed—the oaks always on the high eroding banks; willows, cottonwood, elms and ash on the depositing ones.

Along the Platte where the bur oak forest clothed the sides of the bluffs facing the river, it soon gave way to prairie near their upper slopes or crests through a fringe of shrubs only a few yards wide. Here big bluestem tolerated the shade of open patches of these shrubs and often extended through the ecotone into the edge of the oak forest. In fact, large areas on the upper slopes and tops of the bluffs were a field of battle between grasses and shrubs; seedling oaks were rare.

On north-facing slopes, prairie often extended downward some distance on the ridges between the U-shaped, parallel ravines leading to the banks of the Platte River. The bur oaks farthest up the sides of the ravines were only 15-20 ft high and 9-14 in. in diameter. At a time when they were seedlings and saplings, they had been well protected from the drying southwest winds. The little bluestem prairie gave way slowly to the oaks in the ravines. A very open stand of wolfberry, dogwood and prickly ash grew among the grasses and, with kentucky bluegrass, under the oaks. Oaks increased in both number and size, and spreading outward replaced prairie on the intervening ridges. Woodland shrubs and vines such as gooseberry, black raspberry, grape and greenbrier, became common. But the narrow belt of bur oak was soon replaced by one of black oak, red oak and linden. This occurred first in the ravines but soon became general, and these trees extended downward to the

river. This sequence was repeated again and again on neighboring ridges, although the transition from prairie to bur oak was sometimes more abrupt and through a border of bluegrass resulting from the shade of the various shrubs.

Along the Missouri River the width of the chaparral on the bluffs beyond the bur oak forest in both Iowa and Nebraska varies from a few feet to 0.5 mi or more. The shrubs are fewer and the light values are generally higher near the outer margin of the zone than on its inner one near the oaks. In western Iowa, as elsewhere, bur oak may border the open prairie or give way to a zone of shrubs (Fig. 5).



FIG. 5. Forest-prairie border east of Audubon, Iowa. Hazel (*Corylus americana*) is the chief shrub, with small bur oaks in background. Photo, 1932.

Measurements in many areas of chaparral and prairie over periods of several growing seasons revealed that the shrub community had the higher water content, higher humidity, lower temperature, less wind, reduced evaporation and decreased light intensity. The oak can thrive usually only in protected valleys in the shelter of hillsides. On some bluffs along the Missouri River a strip of red oak and linden may occupy the lower slopes.

The tree communities of western Iowa are distributed along the streams and valleys and are best developed where they are well protected from drying southwest winds.

THE LARGER BOTTOM LANDS AND THEIR VEGETATION

Over the flood plains or bottom lands of the Missouri, Platte and lesser rivers, in addition to trees and shrubs which more or less border the rivers, plants of swamps, marshes, and three communities of grassland occur. Swamp plants live in the abundant shallow lakes and ponds or on the margins of deeper ones. Sedges and rushes occupy the marshes, where the soil is very wet in spring and early summer when it may be covered with several inches of water. Coarse grasses, such as prarie cordgrass or switchgrass, occupy large areas of soil on higher ground than the marshes, but the largest grassland community is that of big bluestem which prevails mostly on second bottom lands where the soil is well drained.

The flood plain is a vast area of level lowland (Figs. 6, 7). Only when one observes it closely are slight changes in elevation noticeable. From the river's margin a distant view is obscured either by steep wooded bluffs on one side or on the other by trees, shrubs and vines of the flood plain forest. Since the apparently nearly level topography actually varies only a few feet below or above the general level, many habitats and various communities seem to the casual observer quite intermixed. Actually, as will be shown, there is a rather definite relationship between the kind of vegetation and the type of habitat which it occupies.



FIGS. 6, 7. (Lower) Republican River near Superior, Nebraska after the great flood of 1935. Much sand was deposited and later blown into low dunes. (Upper) Woodland along the James River in southeastern South Dakota and extensive hay meadows on the flood plain.

DEVELOPMENT OF FLOOD PLAINS

A river makes not only its own bed and channel but also the valley in which it lies is fashioned by the stream. The secular shifting of great river channels is recorded in the conformation of the plain. The flood plain of the Missouri River is 0.5-1.5 mi wide between South Dakota and Nebraska (Figs. 8, 9). In places southward it is 17 mi wide, but varies from 8-14 near the Kansas state line. The larger part of the flood plain in this area, perhaps 80%, is in Iowa.



FIG. 8. Missouri River near Vermillion, South Dakota, showing young growth of cottonwood on a sandbar. The fringe of sandbar willow (*Salix interior*) has been eroded away.



FIG. 9. General view of bluffs facing northward along the Missouri opposite Yankton, South Dakota, showing trees along a ravine.

It is bordered on the east mostly by a broken line of bluffs, but in places only by hills. The channel often lies close to the steep bluffs which form the western boundary of the valley. The river is $\frac{1}{4}-\frac{1}{2}$ mi wide where it begins to border Nebraska. Here the Ushaped valley lies about 150 ft below the summit of the immediately bordering bluffs. In southeastern Nebraska the bluffs bordering the wider, more mature valley are somewhat higher, some extending upward 250 ft. This river borders Nebraska for a distance of about 360 mi but because of its sinuous course the actual length is approximately 500 mi. The general elevation of the flood plain is about 1,250 ft where it first forms the South Dakota-Nebraska line and 850 ft at the Kansas-Nebraska border. The river's gradient is about 1 ft/mi along this portion of its course.

Streams in western Iowa flow more southward than westward (Fig. 1). The course of the Little Sioux River is more or less parallel with that of the Missouri and many of the southwest-flowing streams drain into it. The Boyer River crosses the flood plain north of Omaha; the Nishnabotna and Tarkio rivers run parallel with the Missouri River far into Missouri before they empty their water into the main stream.

In Nebraska the general slope of the land is east and this determines the direction of flow of the rivers. The Platte, in the central part, is largest. This broad, shallow stream generally has low banks, but 20 mi or more from its mouth (Plattsmouth) the flood plain becomes narrower and the bordering hills and bluffs steeper. Its main northern tributary, the Elkhorn, flows southeast from its source in sandhill lakes and joins the Platte only a few miles from the Missouri. Salt Creek enters the Platte from the southwest but most of the southeast area is drained directly into the Missouri by the Weeping Water and Little and Big Nemaha Rivers. The Big and Little Blue Rivers reach the Missouri through northeastern Kansas by way of the Kansas River. Bluffs border many of the larger streams in part but often the valleys are bounded only by hills. Each river has its flood plain and many smaller streams meander through a plain 0.5 to 3 mi wide before entering the larger one of the Missouri.

The first bottom land of the flood plain is an expression of former channels of the river and materials which they constructed. Topography of the second bottom may result from the leveling processes of sedimentation by slack water from the river's flooding. Drainage out of the hills is mainly that of many small streams, often fed by numerous springs, that do not cross the flood plain but fill the ponds and lakes with sediments from the upland.

A stream or river when it rises and reaches the over-bank stage inundates the adjacent valley floor. When the overflow is spread out over the flat land its velocity is quickly and effectively checked. The heavier soil particles carried by the water are deposited along the immediate borders of the channel. These deposits take the form of low but distinct ridges, termed natural levees. They border the channel and remain after the flood has subsided. As flooding is repeated they are built higher until they become the most visible features of some valley floors. They may attain heights of 4-14 ft or even more but their heights are small compared with the depths of the channel. In the Missouri River this depth may be as much as 30 ft.

The part of any stream valley which is inundated during floods is a flood plain. In the course of floods the entire flood plain may be covered by a thin mantle of sediments which settles out from the lakelike shallow flood water that carried suspended finer silt and clay from the river.

A stream that rises in flood may overtop the natural levees in its down stream course. When the levees are breached at a weak point, the water flows rapidly down their outer slopes, which are much steeper than the gradient of the channel, and continues outward through new channels, leaving the old one with diminished discharge. Often the old channel is ultimately abandoned as a new one is formed. The new channel offers a lower level or a shorter course and it therefore gains on the old one

until it carries the greater volume of water. It is rapidly widened and deepened by the swift current. In the older one the current is slower and the sand and silt is dropped and the bed built up. Often a bar is built across the old channel which may then become a lake or slough. Sometimes several channels are developed forming a braided river. During such great floods the entire valley floor may be inundated except the trees growing along the main levees of the main channel. When a main stream breaks through a natural levee following ice jams, heavy rains or rapid melting of snow, the high-water stage has terrific force and may cause great damage.

Exceptionally high floods may inundate portions of the flood plain that the waters of usual spring floods do not reach. For example, a great flood occurred on the Missouri River in the spring of 1881. "The extensive bottom land was plastered with mud and sand: sites of farm houses were marked by piles of debris and by ruined chimneys; staunch barns were undermined, tilted, and rent with unequal settling, their doors and lower planking were torn away, and banks and bars of rotting grain marked the direction of the flood; the great corn cribs, hundreds of feet in length, were represented only by heaps of half-decayed corn . . . the fences were reduced here to scattered timber, there to tangled loops of barbed wire clinging to the stronger posts and clasping the carcasses of cows, horses, and swine; the railway track of a month before was scattered to right and left in hundred-yard links of rails and ties, the bent and twisted rails still grasped by a tie or two . . . in short, the fair land of a month before was replaced by a picture of utter desolation . . . one of the many reminders that man may not encroach upon the domain of a river with impunity" (McGee 1891).

Sinuous bends in a stream's channel, if they are fairly even and regular, are known as meanders. The Missouri and Platte are notable examples of meandering rivers. In meandering and shifting their courses, rivers may repeatedly abandon their channel and cut a new one in such manner as to leave a great loop in the river as an oxbow lake in the area of its flood plain. The oxbow is formed when the river cuts across the neck of a big bend or meander. As the lake is slowly filled with sediments, chiefly silt and clay, it becomes a pond and then a swamp or marsh. According to Longwell & Flint (1955) the river does not shorten its course especially by such cutoffs, because the lost mileage has been balanced by the enlargement of other meanders.

With each overflow, the natural levees on the river's banks become higher and the back-swamp more poorly drained, since this portion of the flood plain has not been elevated as rapidly as the stream bed. Where the natural levees come in contact with the uplands they prevent the escape of water collecting behind them and temporarily, pond or marsh conditions develop. At the edge of the valley, drainage out of the hills is mainly that of small streams that do not cross the flood plain.

As explained by Harper (1938) water in the

channels of tributaries flowing into the main river is also affected by the silting. Water in the channels of these streams must attain a considerable depth before it can flow into the main river, consequently the valleys have not only been filled with sediments but natural levees may also develop from the edge of the valley to the junction of the tributaries with the larger stream. The combined effect of the cross levees prevents the escape of flood water collecting behind them. Materials suspended in runoff water flowing through these areas settles in the quiet water. Thus, deep layers of sediment may be formed.

Rivers, both large and small, as they flow through erodable land develop a flood plain. Such areas are commonly designated as bottom lands and more especially as first or low bottoms and second or high bottom lands. It has been estimated from several soil survey maps that along its course the Missouri River has 40 to 50% first bottom land. On first bottoms, especially within a mile or two of the stream, the river may occasionally change its course; but elsewhere such changes are to be reckoned in terms of hundreds or even thousands of years.

The Missouri River bottom is a nearly level plain of alluvial sediments. The topography is uniformly level, except in the relatively small areas where low ridges and shallow swales and slopes along the edges of old channels cause gentle undulations. Infrequently deposits of sand have been blown into low hills in local places. Usually the land has slopes of less than 2 to 3%. Meander scars are characteristic features of flood plains.

Fig. 10 was taken from a portion of the Craig, Mo.-Nebr. Quadrangle Sheet of 1920, supplemented by information from Corps of Engineers, Rulo to Yankton Survey of Missouri River, 1946-1947. It shows the braided and meandering Missouri flowing near the foot of bluffs which, as indicated by the contour lines, extend upward 150-200 ft above the flood plain. Also shown are cut-off lakes, the abundant larger marshes, sandbars (dotted areas) and islands, and a tributary river (Tarkio) and Little Tarkio Creek meandering across the flood plain. Here the valley varies in width from 5 to 14 mi. West of the main river and southwest of Bigelow the altitude is 861 ft and east of it, near the cut-off lake, 859 ft. It decreases only a few feet (to 858) near the Tarkio River but increases to 862 ft beyond the river. Thus, differences in elevation of only a few feet occur on this portion of the flood plain. The small flood plain of Squaw Creek (upper right), and the wide one of the meandering Nemaha River as it cuts through the row of bluffs (lower left) are shown.

FLOOD PLAIN SOILS

Low bottoms of the Missouri River present the following mixed alluvial land: Albaton, heavy soil (clays); Onawa, heavy soil of medium and moderately coarse clay over silt and sand; Haynie, soils of medium textures (loams and silts over sand); and Sarpy, a coarse sandy soil. Sandy soils often contain good supplies of most nutrients but are low in organic mat-



FIG. 10. A section of the Missouri Valley between Missouri and Nebraska just north of the Kansas-Nebraska boundary. The squares each represent 1 sq mi. Explanation in text.

ter and nitrogen content. These alluvial soils have been formed from recently deposited sediments and they lack distinct horizons. But they commonly do have layers which reflect the history of the stream. They usually occur near the river channel and are subject to occasional or frequent flooding, but they are moderately to well drained between overflows. They are occupied partly by trees, mostly willows and cottonwood, shrubs, sedges and rushes, and, in part, by various coarse, hydric grasses.

High or second bottoms of the Missouri and similar large streams present poorly drained Luton and Wabash clays and Lamoure silty clay loam. The Luton soil, a Wiesenboden or wet meadow soil, occurs mostly on the wider and flatter parts of the flood plain, usually near the bluffs. On these wet meadow soils cordgrass, switchgrass, and wild-rye thrive. On Salix soil, a Brunizem (Prairie) soil of medium to moderately fine silt loams and clay loams that are mostly well drained, big bluestem is dominant. This soil occupies the slightly higher parts of the upper flood plain. Second bottom soils are flooded only rarely (Fig. 11).

Soils present in the small bottom lands of tributary streams are the somewhat poorly drained Leshara silty loam and Colo silty clay loam and the moderately well drained to well drained Kennebec and McPaul silt loam. These soils are mostly occupied by tall grasses chief of which is big bluestem. Trees often occur along the stream channel. The well



FIG. 11. Cross-section of the Missouri River flood plain showing position and relative elevation of the various soils in relation to the river. The Luton, Wabash and Lamoure soils are poorly drained because of runoff and perhaps seepage from hills and bluffs. Here lakes, ponds and marshes are frequent.

drained Judson silty loam at the foot of slopes furnishes an excellent habitat for big bluestem prairie.

Thus, a large number of soils, some water-logged, some poorly drained, others well drained and well aerated compose the bottom lands. Moreover, flooding, draining, and accompanying removal or deposition of soil are cyclic catastrophes. It seems clear to both the ecologist and the pedologist that it is not soil type per se that determines the kind and amount of native vegetation but rather aeration and constancy of water supply of these mostly productive soils that directly affects the vegetation. Generally these bottomland soils are neutral to slightly alkaline in reaction. When the land is placed under cultivation it is found that nearly every square mile presents several soil types.

A generalized diagram across a large flood plain is shown in Fig. 11. The width is several miles; the horizontal lines indicate the relative elevation or depression of the various portions of the flood plain. Separation of first from second bottom is often much less abrupt than is shown in the figure, but the difference in elevation is usually 10 or more ft. With a 10-ft rise in flood, the river water enters the channels of the first bottom. When the rise is 20 ft the first bottom is completely inundated and water enters the channels of the second bottom. A 30 ft rise in the river inundates all but the highest areas on the second bottom, and the entire valley may be covered with several feet of water in extremely high flood, but this happens very rarely. Fig. 11 is representative of conditions along the Missouri River in most places between Iowa and Nebraska. The writer is indebted to John Elder, Conservation and Survey Division, University of Nebraska, for figure 11 and to the Soil Conservation Service for much information on soils (Cf. Simonson, Riecken & Smith 1952).

FLOOD PLAIN FOREST

Flood plain forests along the larger rivers consisted very largely of cottonwood and willows. Along the Missouri they ranged from the water's edge over natural levees, to a distance of 1/8 to 1/2 mi from the river above Plattsmouth and to somewhat greater distances, in places, southward. In addition they bordered abandoned river channels, lakes and ponds. In the river they clothed great sandbars, and sometimes covered many acres of alluvial deposits on the inner or lower flood plain. The remaining area of the low, wet, first-bottom land was occupied by lakes, ponds, marshes, and in places by a luxuriant growth of coarse grasses often alternating or intermixing with various shrubs.

On the second bottom, forest occupied a very minor portion of the area. Here the supply of soil moisture resembles closely the type now found in prairie elsewhere. Soil development, with rare exceptions, clearly took place under a continuous cover of grass. It is possible that prairie fires had some retarding influence upon tree growth, but it seems more probable that the natural environment of moderate rainfall (23-33 in.), dry winds and long periods of summer drought, which characterize the prairie climate, were the determining factors.

Sandbar willow (Salix interior) is the first tree or shrub in this area to grow upon sandy or muddy banks of rivers, streams and lake shores. Its extremely abundant, fiber-like roots enable it to maintain a hold on the soil. This small tree, usually about 20 ft high, has a slender trunk 2-3 in. in diameter. In dense stands, which result from its spreading by long stoloniferous roots to form thickets, it is commonly dwarfed into a shrub only 5-6 ft high. Branches are slender, erect, and flexible. The elongated narrow leaves are light yellow-green. Saplings 3-6 yrs old often occur at the rate of 8-10/sq ft. Usually there are few other plants in such dense stands. This willow is common in drying lakes and ponds, often intermixed with cattails and river bulrush, and also in marshes. Thickets of willows covering many acres are not infrequent. Sandbars in great rivers are often completely clothed with this species (Figs. 12, 13). Because of its stabilizing the soil, they may eventually become more or less heavily wooded. At Fremont and a few other places along the Platte and on several islands in the upper Missouri in this area, red cedar (*Juniperus virginiana*) also occurs on the lower flood plain and on islands in the river.



FIG. 12. A sandbar in the Missouri River mostly covered with sandbar, black, and peachleaf willow, with a few (taller) cottonwoods (*Populus sargentii*).



FIG. 13. Cottonwoods on Missouri River flood plain, showing their abundance along the small cut-off at the right.

Rivers are forever cutting away their banks in one place and depositing soil in another. Where the Missouri River forms a great bend, one may have an unobstructed view of the river-bank vegetation. The eroding side is often treeless, the woody vegetation having been undermined and swept away. Standing in the tall prairie grasses, one may look down from the eroding bank, where the water is deepest and moving most rapidly, and up and down the river for a mile or more. On the opposite or depositing shore one observes the continuous low zone of young sandbar willows, perhaps 50 yds wide. Beyond is a similar zone of older and taller willows, and still beyond are complete stands of tree willows (Salix amygdaloides, S. nigra). Still farther from the water's edge, a forest of stately cottonwoods towers upward to form the background of this magnificent scene.

The two species of tree willows are commonly 20-40 ft tall and 8-20 in. thick. They prefer the wet lower banks of streams and borders of lakes, ponds and marshes. They are intolerant of shade and usually form a border to the cottonwood forest which follows the river all along its course.

Cottonwood is the most typical tree on the banks of great rivers and often the only one on eroding shores where the fringe of willows on lower ground has been swept away. It is the only large tree on the banks of the Missouri and Elkhorn Rivers north of central Nebraska. Cottonwood grows rapidly and reaches a height of 70 ft or more, with trunks 3-6 ft in diameter. Where well lighted, as on the river margins or in open stands, branching begins low and scarcely higher than the shrubs. But in the forest the straight, erect or more or less leaning trees are free from branches to a height of 20-30 ft. Young trees have smooth, light yellow-green to nearly white bark, but on old ones it is ashy-gray, thick, and deeply furrowed into broad, rounded or narrowedged ridges broken into scales (Fig. 14).



FIG. 14. Mature cottonwood trees with undergrowth of roughleaf dogwood (*Cornus drummondi*) on flood plain of Platte River.

Although flood plains usually bring to mind broad, level land, the site of this forest type is often very irregular. The river in flood has built up ridges and bars often 10 or more feet high running outward in all directions, with valleys, ravincs, ditches, ponds and marshy places, all indiscriminately intermixed. Often the trees are scattered rather thinly, brush is only moderately abundant, and patches of lowland grasses may occur (Fig. 15). In other places trees are more closely spaced and thickets of young trees, shrubs and vines are so abundant that one can make his way over the irregular terrain only with great difficulty. An example of each type will be described; all intermediate conditions prevail.

As one proceeds from the water's edge, the thickets of low-growing willows give way to older ones, perhaps 20 ft high and less thickly spaced. Dense masses of various vines trail over the ground, climb up the trees and spread extensively through their branches. Frost grape is often the most abundant, although poison ivy and virginia creeper are



FIG. 15. View of the flood plain with cottonwood and willows and young elms on the Missouri near Omaha.

usually plentiful. The weight of the grape vines is so great that the willows are often bent down and their stems, although 2-3 in. thick, broken off at a height of 5-8 ft. Added to this tangled mass of vegetation are tree willows, many of which are leaning or have fallen and are overrun by false buckwheat (*Polygo*num scandens).

Next one may encounter a depression with a thicket of dead sandbar willows or areas of tree willows 30-35 ft high with trunks 5-11 in. in diameter. Beneath is a tangle of seedlings of cottonwood and willows. In more open places various shrubs and vines form a tangled mass of vegetation.

Wetter areas of a few square yards to several A in extent occur. Where the light permits its growth, nearly pure stands of reed canary grass (*Phalaris arundinacea*) may be found. By midsummer the leaves of this 5-8 ft high grass are dead and the plants often lodged, thus again making walking difficult. More often brush, consisting of dogwood, indigobush and prairie rose (*Rosa setigera*), and scattered willows, young cottonwoods and elms are intermixed. In still other places shrubs, cordgrass, switchgrass and dense patches of oxeye, american germander (*Teucrium canadense*), or tall sunflowers may occur. Thickets of plum, young cottonwood and elm are often so dense that there is no undergrowth.

Pools with cattails, arrowheads, and bordering sedge marshes may alternate with groups of tall, stately cottonwoods on the adjacent ridges, or with a dense undergrowth of patches of shrubs and vines.

Often the undergrowth of poison ivy is more or less continuous, at a height of about 2 ft, with vines climbing 20-30 ft on the trunks of trees. Lateral branches of the ivy sometimes reached outward 2-3 ft. Cottonwoods are differently spaced than are trees of upland forest. Near the river they nearly always occur on ridges in scattered groups of 2-10. The trees in a group often appear to be even-aged.

Elsewhere on the plain there are often wildernesses of sandbar willows, thriving, dying or dead, patches of tree willows with thickets of sapling red elm so thickly grouped that they are impenetrable. Similar patches consist of various shrubs-roughleaf dogwood, indigobush, wolfberry (Symphoricarpos occidentalis), sumac, prairie rose, prickly ash, elder (Sambucus canadensis) and others-all intertwined with vines of grape, virginia creeper and greenbrier. Interspersed are scattered trees, mostly young, of ash, mulberry (Morus rubra), boxelder, and an occasional honey locust. In this mixed vegetation grasses and forbs vary from complete absence to isolated bunches or small patches. The competition for light is so great that these plants elongate abnormally; species of smartweeds, american germander, western ironweed (Vernonia fasciculata), and tall goldenrods reach heights often twice those usually attained.

Added to the preceding are occasional masses of debris deposited during floods, fallen branches, uprooted trees, fallen logs, and occasionally dense stands of giant ragweed (*Ambrosia trifida*) 10-12 ft high, and other ruderals, often in abundance. This description may give a fair idea of the denser type of the flood plain forest of the Missouri and Platte Rivers.

Many cottonwood forests are far more open; one can walk through them with only minor deviations in his course. The large trees are widely spaced, often in small groups. Shrubs are abundant but occur singly or in small dense patches. Often enough sunshine occurs in openings to permit the growth of grasses. On many high, eroding banks where willows are few or none, great clumps of wild-rye, switchgrass and even big bluestem grow among the cottonwoods. But mostly cottonwoods alone occupy the banks; then the sandy soil is covered with a thin layer of fallen leaves and other debris. Elsewhere, a usually discontinuous understory of small trees, numerous shrubs and a layer of forbs prevail.

Scattered over the lower flood plain far from the river many cottonwoods of large size occurred. Some were 5-6 ft or more in diameter and 60 to 85 ft tall. Ring counts of stumps of similar trees revealed that they were 70-80 yrs old. On better drained alluvial soils farther from the river banks, many other forest trees are common. They are mostly red and white elm, ash (including white ash (*Fraxinus americana*), boxelder and hackberry. They all prefer rich alluvial soils to river sand. Large trees are often infrequent; dead or dying saplings are common, resulting from poor soil aeration and deep shade. But on well drained, rich bottom lands, well developed specimens are abundant. Walnut (*Juglans nigra*) is not plentiful except in the south, and there also sycamore (*Platanus occidentalis*) is a common flood plain tree.

Adjoining the flood plain, on the better protected slopes the red oak-linden community prevails along the Missouri River almost to Sioux City. It also extends 20-30 mi along the tributaries entering the lower portions of this river, linden ranging quite beyond the red oak. Where the stands are thick, fallen leaves cover the soil beneath the trees more or less completely.

It has been shown that flood plain forest is represented, even if poorly, along nearly all of the streams in the area. Willows represent the first stage; a little farther down the stream they become associated with the cottonwood and boxelder. On better developed flood plains, usually only a few miles from the head of the stream, red and white elm, and green and white ash become plentiful. The preceding species with the addition of hackberry and walnut and perhaps soft maple (Acer saccharinum), honey locust, kentucky coffeetree (Gymnocladus dioica), and sycamore (Platanus occidentalis) (southward) compose the typical flood plain forest of the broader more mature flood plains. Where the larger streams flow into great rivers much of the flood plain was forested. But northward and westward, under decreased rainfall, trees were generally confined to the moist, protecting stream banks.

The willow-cottonwood portion of the flood plain



FIG. 16. Well developed trees of american elm (Ulmus americana) on the flood plain of the Big Nemaha near Falls City, Nebraska. The largest tree is 3.5 ft in diameter and 95 ft high. Photo in 1928.

forest is especially typical of the Platte and Missouri rivers. It extends over low sandy banks, sandbars, abandoned channels and elsewhere. "A later development is shown by the growth of such species as Acer negundo, Ulmus americana, U. fulva, Fraxinus pennsylvanica, and Juglans nigra. These in turn may finally be replaced by Tilia americana, the elms often remaining as codominants" (Aikman 1929). The usual flood plain species occur on more stable and better drained soils of the broad flood plain between the bordering wooded hillsides or bluffs (Fig. 16). "The flood plain associes reaches its best development along the larger streams in the southeastern part of the area. . . . Since the shade is denser, fewer of the less tolerant species are found. The trees are much larger and in every way the flood plain forest better developed. Secondary species are Fraxinus americana, Padus virginiana, Gymnocladus dioica, Aesculus glabra, Celtis occidentalis, and Platanus occidentalis. The shrub stage is not as prominent as in the previous stage because of reduced light" (Aikman 1929).

According to Aikman, in the absence of devastating floods over long periods "the flood-plain may finally be built up to a place where the soil becomes sufficiently well drained and aerated to permit the growth of climax dominants. . . . The advance of red oak and especially linden into such areas has been repeatedly observed and sufficiently studied to show the trend of development toward climax forests."

Common shrubs of the flood plain forest, which also extend far beyond the forest margin and intermingle with coarse grasses, are as follows; those near the end of the list are usually of least abundance.

Cornus drummondi	Rhamnus lanceolatus
Boughleaf dogwood	Buckthorn
Amorpha fruticosa	Rubus occidentalis
Indigobush	Black raspberry
Symphoricarpos occidentalis	Rosa setigera
Wolfberry	Prairie rose
Symphoricarpos orbiculatus	Zanthoxylum americanum
Coralberry	Prickly ash
Rhus glabra	Cornus stolonifera
Smooth sumac	Red osier
Prunus americana	Euonymus atropurpureus
Wild plum	Burningbush
Sambucus canadensis	<i>Rubus allegheniensis</i>
American elder	Common blackberry
Ribes missouriensis Wild gooseberry	

Roughleaf dogwood is one of the most abundant. Dense stands may skirt the forest edge and thickets 8-10 ft high with little undergrowth may extend outward over many square rods. Indigo bush, of similar height, is most abundant around ponds, in marshes and on the wet banks of ditches. Elder also thrives best in wet places. Smooth sumac mostly borders the sunlit openings or occurs on the forest edge. In the southern part of the area buttonbush (*Cephalanthus occidentalis*) grows in low wet soil.

The following woody vines were usually common and often abundant: frost grape (Vitis vulpina),

bittersweet (Celastrus scandens), greenbrier (Smilax hispida), poison ivy (Rkus radicans), virginia creeper (Parthenocissus quinquefolia) and virgin's bower (Clematis virginiana).

EXTENT OF FLOOD PLAIN FORESTS

The writer, in 1954, summarized forest and prairie on flood plains as follows: "On the wide alluvial bottomlands of the larger rivers, of both eastern and western prairies, the forests were often limited to relatively narrow strips along the channel and the abandoned oxbows, alternating with strips of prairie." This is in accord with the observations of early explorers, pioneer settlers, and early land surveys, and is confirmed by studies of scientists in the early part of the present century.

Bradbury (1809) reports: "I availed myself of this opportunity to visit the bluffs [across the Missouri River near Omaha | four or five miles distance from us, on the north-east side. On approaching them I found an extensive lake running along their base, across which I waded, the water in no part reaching higher than my breast . . . Its surface was much covered with aquatic plants. On gaining the summit of the bluffs, I was amply repaid by the grandeur of the scene that suddenly opened to my view . . . and looking into the valley of the Missouri from an elevation of about two hundred and fifty feet, the view was magnificent: the bluffs can be seen for more than thirty miles, stretching to the north-eastward in a right line, their summits varied by an infinity of undulations . . . The flat valley of the Missouri, about six or seven miles in breadth, is partly prairie but interspersed with clumps of the finest trees through the intervals of which one could see the majestic but muddy Missouri."

Schaffner has been intimately acquainted with the prairies of Kansas since 1871, at a time when the original conditions prevailed. He states in 1926: "The first bottom of river flood plain, where a normal soil had developed, was largely occupied by a typical *Andropogon furcatus* prairie, due to the action of prairie fire which was continually destroying the forest belts developed in the river bends and confining them to narrow strips . . . The second bottom was ordinarily too dry to permit of tree growth. Only the low flood plain, deep ravines, and steep protected slopes are potential forest habitats in the absence of fire."

Sampson (1921) lists numerous extensive grassland areas along the Mississippi and Illinois rivers in Illinois, and Turner (1934) states that the flood plain forest is confined to a belt or zone a few hundred yards to a half mile in width paralleling the river channel or surrounding ponds and lakes. The landward side of this forest type merges into a grassland association.

It is believed that along our section of the Missouri River the flood plain forest, shrubs and coarse grasses occupied most of the first bottom but that the second bottom was nearly all covered with prairie. Exceptions of course occurred around ponds and

lakes and on poorly drained land. It has previously been pointed out that the well drained Salix soil has developed under a cover of prairie grasses, and the less well drained Luton soil under coarser, wet meadow grasses (Fig. 11).

The Missouri and Platte rivers have very wide valleys and although the bordering bluffs and hills furnish protection against the prairie climate, this protection does not extend throughout their width (Fig. 17). In fact, some of the best developed flood plain forests, with a great variety of trees, occur in the protection afforded by wooded bluffs and steep hillsides where tributary streams with relatively narrow flood plains join the main rivers. It is interesting to note that trees on the upper edge of the protecting slopes are of lower stature than those on the lower slope. Indeed, the canopy of trees bordering streams is often nearly level.



FIG. 17. Flood plain of the Platte near Fremont, Nebraska showing trees along the river in background and the wide expanse of grassland. Photo July 15, 1929.

The kinds of flood plain communities, in addition to forest, and their interrelations are of importance to an understanding of grasslands.

SWAMPS

The reed-swamp stage of the hydrosere is well represented in lakes and ponds both large and small which occurred by the thousands and were especially widely scattered over the flood plains of the principal streams. A lake may be defined as an inland body of standing water occupying a basin; a pond, as a lake of slight depth. Swamps are places where the normal summer water level is continuously above the soil surface.

The dominant species of swamps are relatively few; all are large, coarse perennials. They are great bulrushes (*Scirpus ralidus*, *S. acutus*), river bulrush (*S. fluriatilis*), broad-leaved cattail (*Typha latifolia*), reed (*Phragmites communis*), bur reed (*Sparganium eurycarpum*), arrowhead (*Sagittaria latifolia*) and water plantain (*Alisma*). "A peculiar feature of marshes [swamps] of this type is the readiness with which the individual facies may become isolated, or localized, notwithstanding their coherency in marshes [swamps] of considerable extent (Pound & Clements 1900)." While these dominants are often intermixed, much more frequently one species may occupy vast areas almost to the exclusion of others. Plants which root on the bottoms of swamps occupy definite places, which are related to the depth of the water, silting, and characters of the substrate. They form definite and often pure communities. The great bulrushes usually grow in the deepest water, sometimes in excess of 6 ft, cattails at intermediate depths, and reeds in the shallowest. All have large, much branched rhizomes, and where establishment of seedings is unsuccessful invasion is still possible.

Swamp plants have such a wide distribution and are so conspicuous that they are known by most students of botany. Hence, only brief descriptions and emphasis on certain features will be given.

Scirpus validus and S. acutus vary greatly in stature. The narrow, terete culms on the edge of drying lakes may be only 3 ft tall and less than ¼ in. in width; in the most favorable habitats they are 7-11 ft high and ¾ in. in basal diameter. They are perennial from tough, slender or stout rhizomes. Often 8-12 culms occur per sq dm. But usually the culms are more openly spaced even when in dense clumps. Vast areas of river banks, swamp land and shallow water were occupied by great bulrushes previous to the drainage of the flood plain. In many lakes they bordered the shores in water 1-5 ft deep continuously for several miles.

Cattail (Typha latifolia) is one of the most common and abundant species of swamps. Where shallow water permanently covers the surface of the soil it almost always occurs. The plants grow thickly in dense, mostly pure stands, yet the individuals do not seem crowded. This results from the nearly erect position of the leaves and the spacing of the clumps along the large thick rhizomes. If the habitat is congenial they spread rapidly to occupy the space; if it becomes dry, the plants are greatly stunted and finally die. Height varies greatly, often it is 5-7 ft above the water level, with some leaves extending well beyond the spikes. But robust plants more than 9 ft tall with basal dimensions of 2x4 in. and about 14-in.-long leaves up to 3/4 in. in width are not uncommon. Cattails often border ponds in a wide zone, and near the shores of lakes they often extend in shallow water as a continuous stand for miles. Fassett (1940) states that propagation by rhizomes is so efficient that an entire community may develop from a very few plants. Enormous amounts of debris result from the death of parts above ground in winter.

Aside from other swamp dominants, cattail stands usually have few other species, except the free-floating duckweeds (*Lemnaceae*) which are present from early spring to late fall. The narrow-leaved cattail (*Typha angustifolia*), of common occurrence here mostly since 1900, is far less abundant.

The reed (*Phragmites communis*) occurs in pure stands in swamps and on banks of streams, where many hydric species, common elsewhere, fail to thrive. This coarse perennial grass has a complex system of rhizomes, which may occupy the soil 8-10 in.

in depth; erect culms are 8-12 ft tall. In addition, very long, horizontal stolons may occur. Always conspicuous because of its rapid growth and great stature, it is especially so during flowering, when the long hairs of the spikelets develop in such manner that the whole flowering portion is a silky mass.

Some experimental work has been done at Lincoln, Nebraska, to test the establishment and competition in three typical swamp communities where Scirpus validus, Typha latifolia and Phragmites communis grew. Separate communities of bulrush and cattails grew along a sluggish stream and reeds about a pond. Reciprocal transplants were made during a period of three years (1923-25). From the results it was concluded "Although both Scirpus and Typha are occasionally found scattered through the Phragmites community in nature, they are to be regarded as relicts. The water content of such areas is too low for them, especially in late summer of dry years, and the dense and continuous layer of rhizomes of Phragmites practically prevents their invasion . . . The paramount factor in their elimination is shade, the great stature and broad spreading leaves of the reed-grass reducing the light intensity to a decisive degree (Clements, Weaver & Hanson 1929).

River bulrush (*Scirpus fluviatilis*) inhabits river banks and shallow water and is very widely scattered over the flood plains (Fig. 18). The abundant, thick rhizomes of this perennial promote rapid spreading. The coarse, stiff stems are triangular in cross-section and reach heights of 4-6 ft or more. The long leaves



FIG. 18. River bulrush (Scirpus fluviatilis).

spread widely. This bulrush occupies great areas of swamps and is sometimes intermixed with species of marsh plants.

Scirpus attorirens is an abundant bulrush scattered widely in wet areas over the first bottom land. It is a coarse perennial with thick rhizomes and grows in dense tufts to a height of 3-5 ft. The 8-10 leaves, about 0.5 in. broad, are mostly on the lower portion of the culms. It usually occurs in places somewhat wetter than those occupied by cordgrass. The dark-green foliage and abundant brown spikelets, the scales becoming black with age, makes this plant conspicuous both in dense patches and when intermixed with other species.

Scirpus maritimus is a perennial rush of very common occurrence, usually in shallow fresh water and in alkaline swamps. The rhizomes that produce the 3-angled culms also develop tubers. The plants in figure 19 grew in a pure stand covering a 0.5 A; the 4 in. of water darkened the base of the culms which reached heights of about 2.5 ft. The spikes are not yet fully developed.



FIG. 19. Scirpus maritimus (left) vith spikes in early, stage of development. Iris versicolor (right) about 2.5 ft tall on June 12.

Scirpus americanus is also a perennial rush which occurs in shallow water or on very wet soil. From the long, tough rhizomes, triangular, stiff culms extend upward to a height of 3-5 ft. The sparse leaves are 12 in. or less in length. The single to several grouped spikelets appear to arise from the side of the culm near its end, since the single bract is a continuation of the culm. This rush is often abundant. Bur reed (Sparganium eurycarpum) has stout, erect leafy stems usually only 2-4 ft tall (Fig. 20). The leaves are shallowly and broadly triangular in cross-section. The plants grow in shallow water, usually in extensive, dense stands and they are of very common occurrence.



FIG. 20. Sweet flag (*Acorus calamus*) (left) 3-4 ft tall with linear spadix covered with yellowish-brown flowers. Bur reed (*Sparganium curycarpum*) (right) about 3 ft tall in fruit.

Arrowhead (*Sagittaria latifolia*) often grows in the shallow water or mud bordering the cattail zone in belts a few feet to many yards in width and an A or more in area. A dozen leaves 8 in, wide and 12-18 in, long may be produced per plant. They form dense stands with a nearly complete foliage cover. In the soil there are dense mats of roots, and rhizomes with tubers 1-2 in, thick (Figs. 21, 22).

Sweet flag (Acorus calamus) not infrequently grows in local, almost pure stands bordering areas of bur reed or arrowhead. Common associated species are spike rush, cursed crowfoot (Ranunculus sceleratus), and water foxtail (Alopecurus geniculatus). It is also found in the wetter portions of marshes.

Other plants of common occurrence and often of great abundance are water plantain (*Alisma*) and, especially northward, indian rice (*Zizania aquatica*). The last is of special interest since it germinates under water, passes through a submerged and floating stage, and then emerges to produce a plant often 7-8 ft tall. A single plant may spread over several square feet.



FIG. 21. Arrowhead (Sagittaria latifolia) growing in shallow water.

The lakes and ponds were also inhabited by water lilies, anchored by roots and rhizomes in the mud 3-8 ft below the water surface (Fig. 23). The leaves sometimes covered the water with floating mats of green over hundreds of acres. Elsewhere pondweed (*Potamogeton*) grew in wide expanse. Equally characteristic were the tiny plants of duckweeds, *Lemna* and others, often so abundant as to form great sheets of green.

MARSHES

Marsh is a term denoting a type of vegetation rooted in an ordinary nonorganic soil that is waterlogged. The water level in summer is close to the soil surface but normally not much above the ground level. In spring or following heavy rains the soil may be flooded. When the soil in swamps is built up to or rises above the water level, marsh plants begin to colonize the areas once occupied by bulrushes and cattails. Phragmites, because of its extensive rhizomes which range in depth from 1 to 10 in., may persist for a time among the marsh plants. This stage in the hydrosere is sometimes designated as the sedge-meadow stage (Weaver & Clements 1938). Small marshes along stream banks and on the edges of ponds have already been mentioned, but they occur most extensively, covering hundreds of square miles, on poorly drained or undrained flood plains of



FIG. 22. Underground parts of arrowhead---roots, rhizomes and tubers.

large rivers. Species of marsh plants, especially various sedges and certain hydric grasses, may occur intermixed with swamp borders of arrowhead, and often the marsh extends quite to the edge of the zone of cattails. On the drier side, marshes give way to cordgrass or other coarse grasses.

Some marshes are inhabited almost entirely by tall species of *Carex, Juncus* and *Eleocharis;* others consist largely of species of hydric grasses such as rice cutgrass (*Leersia oryzoides*) and reed canary grass; but usually they consist of a mixture of species from the preceding genera intermixed with grasses and forbs. Marshes, usually of smaller extent in wet ravines and depressions in wet land, are often entirely populated by forbs, mostly of the smartweed genus (*Polygonum*).

In general appearance marshes do not differ greatly from lowland prairie; the densely grouped mostly perennial and sod-forming species of sedges have grass-like foliage which begins growth very early and attains a height of 2-3 or more feet early in June. The plants frequently grow in open bunches



FIG. 23. Zones of white water lily (Nymphaea tuberosa), bur reed, and sandbar willow.

but rhizomes are common and with the abundant fibrous roots they often form a dense sod. A very large number of species compose the marsh vegetation but only a few of the most abundant ones will be noted.



FIG. 24. Fox sedge (*Carex vulpinoidea*) (right) nearly 3 ft high and in fruit on July 5. A rush (*Juncus tenuis*) (left).

Carex vulpinoidea, fox sedge, grows in dense tufts and alone or with other species forms a compact sod (Fig. 24). The stiff, upright stems have an abundance of long, grass-like leaves. Stands are dense and often nearly pure except for swamp milkweed, fringed loosestrife, and other hydric forbs. The extensive rhizomes produce 5-20 stems per square decimeter and the foliage entirely conceals the soil. The shade is dense and frequently the debris is 5-7 in. deep. As a dominant it may form small patches or cover extensive areas. It often forms distinct zones around ponds or other bodies of water. Early growth results in foot-high plants in April and twice this height in June. When in fruit, in late June or July, plants are often 2.5-3 ft tall. This species is of very common occurrence and often alternates with cordgrass or is intermixed with it as an understory. In hundreds of places that are too wet for prairie grasses, it forms alternes often of such great extent they may compose half of the entire vegetation. Usually it is associated with other tall sedges such as *Carex lasiocarpa*.



FIG. 25. Carex lasiocarpa on May 20, showing both staminate (upper) and pistillate flowers. Height is about 3 ft.

Carex lasiocarpa is a rhizomatous plant with flat, very long attenuated leaves which are often 5 mm wide (Fig. 25). A height of 2 to more than 3 ft is attained late in May. It often forms nearly pure stands over considerable areas, but it is also mixed with other sedges and rushes. It occurs abundantly on wet banks or in shallow water bordering bur reed swamps, and is commonly associated with western water hemlock and stiff marsh bedstraw. Like the preceding species it frequently composes a considerable part of marsh-land hay.

Carex sprengelii is a tall sedge often associated with C. vulpinoidea but it also grows in nearly pure stands. It is abundant along streams and frequently composes much of the marsh vegetation, especially in the northern section of the area. Rhizomes are numerous and the culms are usually less than 3 ft in height.

Carex lupulina forms dense tufts by means of short, stout rhizomes. Figure 26 shows a small portion of an old bunch with a basal area of more than a square foot and a circular top 3 ft in width. The plant is usually 1.5-3 ft tall. The larger leaf blades are 1 to more than 2 ft long and average nearly 0.5 in. in width. The hundreds of cylindrical, pistil-



FIG. 26. *Carex lupulina* with broad leaves and an abundance of pistillate spikes. Height is 3 ft.

late spikes are very conspicuous. It is a characteristic species of shallow swamps and marshes. This species like *C. lurida* and certain others, extends into shallow water on small hummocks of earth and also grows thickly on the muddy edges of ponds.

Carex stricta was once abundant over the area where it formed extensive patches characterized by the culms forming large stools or patches in swales and marshes. Costello (1936), who has made a thorough study of tussock meadows in southeastern Wisconsin, states: "Tussock meadows are dominated by a single species, *Carex stricta*, which produces tussocks that consist of a tuft of leaves and culms at the summit of a pedestal composed of roots, rhizomes, soil, and vegetable debris. New tussocks are initiated by means of rhizomes which grow horizontally from the bases of old tussocks. Individual tussocks may attain a height of 2-4 ft and a diameter of 30 in. They may persist in an area for many years." Marshes were found along the Elkhorn River where the tussocks were elevated above the soil 12-18 in. Since the clumps were separated by distances of 1-3 ft and the interspaces were obscured by the overhanging dense foliage of the 3-ft tall plants, walking was difficult although the soil was not wet. Only a few of the preceding sedges and other marsh plants occurred here. In other places this sedge was found in water about 12 in. deep.

Carex festucacea grows in dense clumps; the long, slender, erect culms hold the flowers quite above the foliage (Fig. 27). It occurred abundantly from very



FIG. 27. Carex festucacea about 2.5 ft tall and in fruit.

wet to rather dry soil. It ranges from soils with relict cordgrass, where it may compose a large percentage of the vegetation, to typical marshy land where it intermixes with other species or grows in pure stands. *Carex hystericina*, *C. lacustris*, *C. cristatella* and *C. interior* are other species of wide distribution and considerable importance.

Among the rushes, *Juncus tenuis* is perhaps the species of greatest abundance. The numerous stems, usually about twice the height of the foliage, are loosely to closely spaced in tufts. They extend outward and upward to approximately twice the height of the narrow leaves (Fig. 24). This perennial is distributed widely from marshes with *Carex rulpinoidea* to wet meadows. On lowland subject to overflow or very high water content in spring it frequently forms extensive patches and constitutes $\frac{1}{4}-\frac{1}{2}$ of the vegetation.

Torrey's rush (*Juncus torreyi*) often occurs in abundance in marshes and wet soil. The conspicuous inflorescence of many heads on one stout, rigid, erect stem is characteristic, as are also the tuber-like thickenings on the underground parts of this rather tall (2-3.5 ft) perennial.

The rushes as a group are far exceeded by sedges both in number of species and in importance in the vegetation of marshes. Several species of *Cyperus*, especially *C. erythrorhizos*, are found commonly in marshes and other wet places, especially in sandy soil.

Eleocharis palustris is the most abundant of the spike rushes. It often occurs in nearly pure stands. Perennial by creeping rootstocks, the annual crop of



FIG. 28. Spike rush (*Eleocharis palustris*) (left) 3 ft high with achenes fallen from the shattered spikelets. *Cyperus erythrorhizos* (right).

terete stems forms much debris (Fig. 28). It varies in height from 8 in. in drier swales to 1.5-3 ft in continuously wet soil or in shallow standing water. This species is most conspicuous in spring and early summer over many acres of low, poorly drained land. The spike rushes, including especially the much smaller E. acicularis, form great alternes with or frequently an understory to other marsh plants and even glow under thin stands of cordgrass. Like most hydrophytes, this species renews growth early. Normally plants are several inches high early in April and a month later the spikes are developing. This is followed by blossoming in June and July. Where Eleocharis palustris is dominant few other plants are associated with it. E. obtusa, a much smaller annual plant without rootstocks, is also common on marshy land.

Smartweed sometimes characterizes marshes in wet ravines and depressions in flood plains and wet meadows. Among the chief species are *Polygonum natans*, *P. lapathifolium*, and *P. coccineum*. The last includes aquatic forms with floating or submersed stems as well as terrestrial forms with erect stems often 3 ft high. Other important species are *P. punctatum*, *P. hydropiper*, *P. hydropiperoides* and *P. pennsylvanicum*. Often singly but sometimes intermixed, they form dense vegetation with few other plants, from muddy stream banks to extensive shallow depressions that are dry in late summer. Height varies greatly, from 1-6 ft. Some species are annuals, others are perennials with creeping stems and well developed rhizomes. Flowers are small but extremely abundant. They vary with the species from greenish to white and pink to rose-red or scarlet.

Since most marsh grasses as well as many forbs also extend widely over the lower flood plain, they will be described along with the coarse grasses of wet lands.

Extensive marshes occurred along the Elkhorn River near Norfolk, Nebraska. One, 80 A in area, was studied in August, 1952, about 3 mi west of the city. Here the flood plain was about a mile wide; the marsh on the first bottom was approximately 10 ft lower than the second bottom where big bluestem prairie was being cut for hay. Everywhere the soil was wet, since the water table was close to the surface. Some places were muddy and in others there was 1-2 in. of standing water. The soil was mostly a sandy loam. Although the topography appeared to be level, there were variations of a few feet. Flat land and low ridges alternated with depressions and small, shallow ditches.

The vegetation consisted entirely of plants characteristic of marshes; bluestem grasses were not found and cordgrass was nearly absent, at least in its characteristic stands. Various carices composed the bulk of the abundant, lush vegetation, which grew to a height of 2.5 to 3.5 ft. It completely hid the soil and had relatively few forbs except in alternes of species of smartweeds. Carex lasiocarpa, C. sprengelii, and C. rulpinoidea were usually the most abundant species. They grew so thickly, in pure stands or intermixed, that walking was difficult. The matured plants were of a bluish-green color; fruits were often so abundant as to add a brownish tinge; the lower portions of the plants were a dull brown, and unlike bluestem prairie there were no flower stalks extending high above the foliage.

Composition of the vegetation varied greatly. In places the tall, stiff, triangular and almost leafless stems of Scirpus americanus were scattered thinly to thickly. Elsewhere it formed dense, extensive and almost pure stands, which indicated somewhat wetter soil. These were demarked by the dark-green color and abundant brown spikelets. Various carices occurred in variable abundance. Among these were C. cristatella, C. lurida, C. lacustris and, in a few places, C. stricta. Spike rushes grew in distinct patches and often in continuous stands. In slightly wetter places, the vegetation consisted of small to large patches of considerably dwarfed Scirpus atrovirens. This bulrush was more or less mixed with various sedges but its brown umbels made it conspicuous. Juncus torreyi was also common and with J. tenuis grew in patches.

Portions of this marsh were clothed with stands of smartweeds often 3 ft high and so dense that most other vegetation was excluded. Chief species were *Polygonum coccineum*, *P. natans* and *P. lapathifolium*. They also intermixed in part with other marsh dominants. Reed canary grass claimed a place in this area, growing in pure stands. Tufts of both northern reedgrass and bluejoint were found and redtop was scattered thinly in places. Species of horsetail (Equisetum) should be mentioned since they were abundantly represented.

Typical coarse marsh forbs were Eupatorium perfoliatum, Asclepias incarnata, Cicuta maculata, Apocynum cannabinum and Aster praealtus. In the understory, where vegetation was less dense, Galium tinctorium, Steironema ciliata, Stachys palustris, Lycopus americanus and Mentha arvensis occurred. Although this list could be greatly enlarged, forbs in general were not abundant. The great mass of hydric vegetation began growth early and soon shaded the soil so completely that many forbs did not thrive.

This great growth of vegetation is utilized by the farmer either as pasture or a poor type of hay, since the soil is usually dry enough to permit hay making in late summer. But where the land can be drained it is far more valuable for farm crops. The present area, like thousands of other marshes, was later drained and is now producing hybrid corn.

COARSE GRASSES OF WET LANDS

Coarse grasses which occupy great areas of flood plains and are intermediate in habitat requirements between plants of marshes and big bluestem prairie, on their drier side, will now be considered. They are predominately prairie cordgrass on the wetter part and switchgrass and canada wild-rye on land less well drained than that occupied by big bluestem prairie. The vigor and great size of these coarse grasses, the extent of their holdings and density of stand can scarcely be overemphasized. Usually cordgrass is rather clearly separated from switchgrass and wild-rye.

Prairie cordgrass (Spartina pectinata), but sloughgrass to the pioneers, is the most abundant grass of the lower flood plain and wet lands wherever they may occur. It almost alone occupied hundreds of square miles along the great rivers and their tributaries throughout the true prairie. It grows on the wet banks of sluggish streams and about ponds but rarely in moist soils except in dry cycles or as relicts in soil which has been drained. On its hydric side this grass is usually bordered by tall rushes, sedges and marsh grasses. A good stand of cordgrass indicates that without drainage the soil is too wet for the production of corn. The soil, like that of the marshes, may be covered with water during a period in spring.

Except for the reed and perhaps eastern gama grass (*Tripsacum dactyloides*), this is the tallest and coarsest grass in the area (Fig. 29). It has a tough, coarse and much-branched system of rhizomes which occupy the surface 8 in. of soil and with the thick, cord-like roots of great depth firmly bind it in place. Stout stems vary from 5-15 mm in diameter. They range from 5-10 ft in height and occur at the rate of 1-3 per sq dm if large, but average about 6 where plants are smaller. The stem has 6-10 leaves with scabrous margins, which are sometimes nearly $\frac{3}{4}$ in. in width and 2.5-5 ft long. The conspicuous panicles are 1-2 ft long and 4-8 in. wide. Maximum flower-



FIG. 29. A typical dense stand of prairie cordgrass (*Spartina pectinata*) on a flood plain. The plants are 6 ft tall; photo July 13.

ing occurs in mid-August. The plants usually form a complete cover and in dense stands almost no other plants are found. Here the foliage to a height of about 2 ft soon becomes yellow and dry. This warmseason perennial renews growth early and extends upward more rapidly than other prairie grasses. Early in June it is usually in the fifth- or sixth-leaf stage and 2-3 ft high (Fig. 30). Yields are large, 3-5 T/A and in some experimental plots they were even greater. When mowed for hay 2-3 cuttings are made annually. Smoothness of the leaves makes the hay difficult to handle; it easily slips off the hayrack or from the haystack.

The ability of this grass to stabilize the soil and resist water erosion is indeed great. Where steep banks of streams, that run bank full during heavy rains, are clothed with prairie cordgrass, the rushing water, once the grass has been lodged, has only slight effect in removing the soil. This has been fully confirmed experimentally; it was shown that soil held by the rhizomes and roots and covered with the wet slippery leaves of this grass reduced soil erosion almost to nil. Moreover it is much less injured by moderate soil deposit than are most grasses; the hard, sharp-pointed shoots push their way upward through a foot of sand or silt. These characteristics, together with its rapid growth from seed, make clear the way in which this grass succeeds in maintaining itself on the ever-shifting soils of the lower flood plain.



FIG. 30. Relative height attained by prairie cordgrass in background and switchgrass (*Panicum virga*tum) in foreground on the Missouri flood plain on June 24.

To keep one's bearings while walking in a great field of cordgrass is extremely difficult because distant vision is quite obscured by the 6-7 ft foliage. When dry, the mass of plant materials, far greater than in bluestem grassland, is an enormous fire risk and any trees or shrubs that had possibly succeded in competition with the grass for light would surely be destroyed by fire.

Eastern gama grass is a tall coarse plant that is abundant and often the sole dominant over extensive areas of wet lands in the southeastern part of this study area. It also forms alternes with cordgrass and is found intermixed with wet land sedges on the one hand and well watered big bluestem on the other. Thus, it has a wide range of habitats from seepage places on hillsides, along ravines, and over the flood plains. It renews growth in March from extremely large and compact rhizomes. Early in May it is 7-13 in, tall and the massive foliage is 3 to nearly 4 ft high by mid-July. Flower stalks appear late in June and increase the total height to 5-7 ft. A single flower stalk may give rise to 3-5 branches, which with the main stem are terminated with conspicuous inflorescences 8-10 in. long (Figs. 31, 32).

Both small and very large circular bunches are produced. These range from 1-2 to 3-7 ft or more in diameter. They produce 15-25 flattened and somewhat woody stems/sq dm. Smaller stems are 2x8 mm in diameter but larger ones may be 5x10 in width. The 7-10 leaves per culm are coarse and frequently 0.5 to 1.3 in, wide and 2-3 ft in length. Under the widely spread and dense foliage few other plants



FIC. 31. Eastern gama grass (Tripsacum dactyloides).



FIG. 32. Rhizomes of eastern gama grass.

survive. When unmowed and unburned a mulch 1 ft deep soon accumulates. Old circular clumps are frequently hollow within and here slight invasion by bluegrass may occur. A single cutting sometimes yields 3 T/A, and often three cuttings are made during the growing season.

Thousands of acres of first bottom land along the Missouri and its tributaries are covered with marshes, cordgrass, and with wet meadows of switchgrass, virginia wild-rye and other coarse grasses. All are subject to occasional flooding and soil deposit. Often the vegetation is considerably mixed and numerous forbs and grasses occur more or less throughout, except where they are kept out by deep shade.

Phalaris arundinacea (reed canary grass) is a

coarse perennial very common in wet places too poorly aerated for most other grasses. The greater height and glaucous color of the foliage makes this grass conspicuous in contrast to the darker green of sedges among which it frequently grows. It often occurs in patches but also spreads widely and the total amount is very great. Like most species of low ground, where competition for light is severe, it renews growth early from a vast system of coarse, deep, tangled rhizomes. New shoots are a foot high in April, and in July the foliage is 2.5-3.5 ft tall and the shade is dense, since the abundant, flat leaf blades are almost 0.5 in. wide. Mature plants range from 2.5-8 ft in height (Fig. 33). The conspicuous panicles are 3-18 in. long and spread widely during flowering. They may turn brown by midsummer; lower leaves to 1.5 ft in height also may die, and with the preceding year's foliage form so much debris that walking in this grass becomes very difficult.



FIG. 33. Bunch of reed canary grass (Phalaris arundinacea) about 6 ft tall.

Leersia oryzoides (rice cutgrass) grows in wet soil or shallow water, often at the edge of zones of arrowhead. It covers extensive areas in marshes, on river banks, and around willow thickets on the flood plain. Its slender, weak culms, often decumbent at the base, reach heights of 2-4 ft. Plants are connected by slender rhizomes. Both leaf sheaths and blades are light green and so retrorsely scabrous that they cut ones hands and tear at ones clothes, in such a manner that progress over the thick grass is slow. L. virginica (whitegrass) is of similar habit but it is much less abundant.

Glyceria striata (foul mannagrass) is found in wet places, especially where big bluestem gives way to wetter grassland. Usually it composes but a small part of the vegetation, but in local areas this tussockforming plant often makes up more than half of the vegetation.

Elymus virginicus (virginia wild-rye) occurs frequently and often abundantly in and near marshes and along streams. Sometimes it forms an understory to cordgrass. Stems of this perennial occur in dense tufts. They are erect, rigid and leafy and usually 3-3.5 ft high. The thick spikes are 2-6 in. long and mostly erect. This important species is also found in open woods and is widely scattered over flood plains. Muhlenbergia racemosa is likewise widely distributed in wet areas and especially near brush or woodland.

Agrostis alba (redtop) is a rhizomatous grass 2-4 ft tall. It often occurs in pure stands, forming alternes with various sedges, spike rush or cordgrass, but it is also intermixed with them as isolated clumps. The rather short flat-bladed leaves do not cast a dense shade, hence an understory of kentucky bluegrass may occur even in places densely populated by redtop.

Poa pratensis, an introduced rhizomatous species, occurs in small amounts more or less regularly in all of the wet-land communities but is often absent or in small amounts in dense shade.

Other grasses of marshes include *Beckmannia* syzigachne (american sloughgrass), Calamagrostis inexpansa (northern reedgrass), C. canadensis (bluejoint) especially northward, Cinna arundinacea (stout wood reed), and Alopecuris aequalis (shortawn foxtail).

Certain forbs are constantly associated with the more open stands of cordgrass and may be intermixed with other grasses of wet land. Fragaria rirginiana, Oxalis stricta and Viola papilionaceae are of low stature. Galium tinctorium, Steironema ciliata, Anemone canadensis, and Teucrium canadense form an understory 1.5-3 ft high. An intermediate layer is composed of Asclepias sullivantii, A. incarnata, Coreopsis frondosa, Verbena hastata, Apocynum cannabinum, and species of Polygonum and Rumex. Very tall plants are Helianthus grosseserratus, H. giganteus, Heliopsis scabra, Cicuta maculata, Silphium integrifolium, Aster praealtus and Solidago altissima. Equisetum arvense is common throughout the bottomlands. The evergreen, solitary or clustered stems of E. hiemale are also common to abundant. They are sometimes about 0.5 in. thick and extend upward 3-5 ft.

TRANSITION TO BIG BLUESTEM PRAIRIE

Panicum virgatum and Elymus canadensis compose a community of coarse grasses which thrive under soil-moisture conditions intermediate between those of cordgrass and big bluestem. Where the land slopes very gradually, broad areas are occupied by this type; but where the changes are more abrupt cordgrass may be separated from the big bluestem community only by a narrow belt of switchgrass and canada wild-rye. Moreover, extensive mixtures occur on both margins. Switchgrass is more abundant southward, wild-rye increases in abundance northward.



FIG. 34. Typical stand of switchgrass 3.5 ft tall on June 24. The old flower stalks of the previous season are 5.5.5 ft high.

Switchgrass is a tall, coarse, sod-forming species. It seeds abundantly and established plants renew growth in April. By early June, the foliage is often 18 in. tall. The dense foliage completes its growth by mid-July (Fig. 34). The leaves are 8-14 mm wide and 1.5-2 ft in length. They are usually 6-8 per stem. Foliage height of mature plants is mostly 3-5 ft but the panicles increase the total height to 5-8 ft. They begin to appear in late July, and at maturity are 1-2 ft long and 16-24 in. wide. More than 300 panicles may occur in an area of 1 sq m. The coarse stems are 6-15 mm thick. This species easily qualifies as one of the coarser flood plain grasses, which occupied thousands of acres of flood plains.

Canada wild-rye attains a height of 3-4 ft by the middle of June. Then the spikes begin to appear. With the elongating stem they add another foot in height. Stems are rather woody and stout. The leaves are broad but only 8-16 in. long. It may form pure stands locally but is more often intermingled with switchgrass. It grows intermixed with cordgrass in wetter places and with indian grass and big bluestem in drier ones. It is of sufficient abundance to rank as one of the more important flood plain grasses.

Examples of the transition follow. On an 80-A prairie of the Missouri flood plain near Bigelow, Missouri, the higher portion was dominated mostly by switchgrass in dense, pure stands or intermixed with canada wild-rye. Relict cordgrass gave way slowly to large bunches of switchgrass and then to the switchgrass sod, except that ribbon-like extensions of cordgrass continued in the switchgrass along a few swales. Virginia wild-rye also became much less abundant. Enough drainage occurred along the high part of the very gentle slope to permit the growth and dominance of big bluestem and indian grass (Sorghastrum nutans). These at first occurred as isolated bunches or more or less circular patches but soon they formed the bulk of the vegetation. Switchgrass and canada wild-rye then became the subdominates.

With the transition from wet, poorly aerated soil to conditions of good moisture and good aeration, there was also a gradual change in other species. Hydrophytic species, as water smartweed and swamp milkweed dropped out. Shrubs, such as indigobush, roughleaved dogwood and elder became rare; but stiff marsh bedstraw, fringed loosestrife and meadow violet remained plentiful in the understory. Species commonly found associated with big bluestem became abundant for the first time.

Along the Platte River many examples were found on the nearly level, wet, sandy soil where big bluestem became intermixed with switchgrass which graded into a nearly pure stand, and then gave way in swales to cordgrass, which, in turn, was replaced on wetter land by extensive marshes. Similar changes on flood plain from big bluestem to switchgrass and then abruptly to enormous bunches of eastern gama grass occurred in Kansas and Missouri. These are examples of scores of other grasslands examined many years ago along the flood plains of various large rivers.

Thus, it seems clear that the transition from cordgrass to big bluestem prairie is nearly always through an area or belt of switchgrass and canada wild-rye. This is also often the same for eastern gama grass.

In the description of lowland vegetation the types or communities have been emphasized. Amount and depth of water and chance distribution of propagules both play a large part in plant distribution. Not only do the same communities occur repeatedly but they are often greatly disturbed and intricately intermixed in patches and zones. The patterns are as diversified as the distribution of meander scars, lake shores and other sites for flood plain forest, or shallow water for swamps, saturated soils for marshes, and areas both large and small of half-dry and dry land.

On the best land of the second bottoms the soil is drained, even if poorly in some places, and the water table is usually several feet below the soil surface. Of the tall grasses composing the lowland prairie, big bluestem is nearly always the chief dominant. Indian grass is of secondary importance as are also switchgrass and canada wild-rye.

Where much sand is deposited on the flood plain the wind often blows it, when dry, into ridges and low hills. Sometimes bluestem prairie, broken and cultivated for several years, has been buried under several feet of sand. Such areas are usually populated by needlegrass (*Stipa spartea*) and various species of grasses and forbs characteristic of the great sand hills of central Nebraska.

Sand hills are developed to some extent on the flood plain along the Republican River. Here may occur sand reed (*Calamovilfa longifolia*), sand lovegrass (*Eragrostis trichodes*), sand dropseed (*Sporobolus cryptandrus*), sand paspalum (*Paspalum straminium*), lance-leaved psoralea (*Psoralea lanceolata*) and cactus (*Opuntia macrorhiza*). All are species common in the Great Plains sand hills. Along the Platte, Elkhorn, and certain other rivers there are many sandy and sometimes gravelly deposits. Most of the alluvium has come from the soils of the uplands in a particular watershed over a long period of time.

Where sandy ridges occur along the Nemaha, the big bluestem on the surrounding heavy black clay loam is almost completely replaced by needlegrass. Areas of many acres on the flood plain of the Missouri are characterized by low sand dunes and sandy soil. Sandy and sandy loam soils along the Platte River are very extensive. Here one finds many of the species characteristic of sand. The type of natural vegetation clearly reveals the extent of the sand. Thousands of acres of sandy lands are used only for grazing. Other less sandy soils, often intermixed with clay loams, furnish vast areas of highly productive land for native hay, as along the valley of the Elkhorn River (Fig. 35).



FIG. 35. Typical flood plain along the Elkhorn River. The great expanse of grassland furnishes an abundance of hav.

Although the flood plain of the Missouri, like the uplands, was early laid out along section lines (sq mi), roads were relatively few and many section lines had none. This resulted in part from open water and wet land but mostly because of the smaller number of farms. In early days the farmsteads were mostly located on the foot-slopes at the margins of the flood plain. But this varied greatly with the width of the plain.

The flood deposits of the Missouri River, including the natural levees, were built up over a long period, but the process has been interfered with by the engineering works (mainly dikes built of earth and concrete) designed to prevent the river from generally inundating its flood plain. The natural levees have been artificially heightened by earth dikes to hold the floods, while at selected points spillways have been built to allow the water of the highest floods to escape harmlessly into natural channels that roughly parallel the river.

After the turn of the century locally organized and controlled drainage districts were formed. The lakes and marshes at the margin of the flood plain were filled with soil from the uplands by directing the water from the hills into them. Here the transported soil settled out and ultimately filled them. The water evaporated from these settling basins and ordinarily did not travel farther over the flood plain. Other low places were built up in a similar manner. In addition thousands of drainage ditches, many 6-10 ft deep, were constructed, often on every section line, to drain the soil and carry the water through proper channels to the river.

Today 75-90% of the land is under cultivation or is pastured (Simonson, Riecken & Smith 1952). Very little of the land is used for production of hay. Furthermore, drainage projects along many of the tributary streams have made the entire flood plain, to the very edge of the old channel, suitable for farming and thus destroyed the natural vegetation. The writer has witnessed much of this change. Modern machinery has contributed greatly to the rate of this destruction of the natural vegetation. Levees or dikes could be built far more extensively and other water control structures and deep drainage ditches made and maintained everywhere with the use of tractor-drawn machinery and draglines. The forests could be removed in a short period of time. To clear the land of towering cottonwoods, the pioneer ringed the bark and thus killed the trees, which were burned standing the next year or two. After the first quarter of the century great bulldozers uprooted the trees which were then dragged into windrows where they were consumed by fire after the wood had dried. In wet and often sandy soil the roots of the cottonwood do not penetrate deeply but spread widely, thus forming a flat-bottomed base.

The descriptions thus far have endeavored to picture the vegetation in its original condition, as a scientific record of the past. Today, even the big bluestem prairie, which covered most of the second bottom, has all but disappeared.

COMMUNITY LIFE IN BIG BLUESTEM PRAIRIE

Typical native grassland even in the more westerly parts of True Prairie has almost been replaced by

closely grazed pastures and plowed fields. This is especially true of big bluestem prairie which occupied the most fertile soil of the lowlands. In the early decades of the present century this prairie was mowed each autumn for its large yield of excellent hay. With an increase in the population, better drainage of lowland soils, and the replacement of horses by the tractor, most of the sod was broken and the land used for the production of cultivated crops. The change has been so widespread that it is now difficult to locate even small representative areas. These prairies were studied from 1918, through and after the great drought of 1934-41, until the land was finally broken.

Big bluestem (Andropogon gerardi) was the most abundant species which occupied the broad valley of the Missouri River and the valleys and ravines of its tributaries. It also grew thickly on lower, well watered slopes. Almost pure stands occurred over extensive areas and this grass alone usually composed 80 to 90% or more of the vegetation. It does not thrive in soil that is frequently saturated, but here gives way to switchgrass and prairie cordgrass.

The total basal cover of the vegetation averaged only 12%; much soil surface remained unoccupied. Yet the foliage was so dense and light so greatly reduced that invasion by other plants was difficult. Growth is very rapid, a dense layer of foliage 3 ft high is produced by midsummer. Then stout flower stalks, each with 9-10 leaves, extend upward 7-10 ft (Fig. 36). In this dense vegetation a few other



FIG. 36. Big bluestem (Andropogon gerardi) about 8 ft tall early in September. A typical scene along many upper flood plains.

grasses, chiefly indian grass, canada wild-rye, and switchgrass occur in small amounts. In addition very numerous perennial forbs ranging from 6 in. to 15 ft in height, grow, flower and ripen seed in interspaces not occupied by the grass.

In early spring the prairie appears dull-brown or gray. The September mowing leaves a stubble 2-4 in. high. Except where mowing is early, there is little aftermath and the soil is usually clothed with only a half inch of litter. Against this drab background the new green blades are very noticeable, and especially societies of forbs in bloom are conspicuous. None attained a height greater than 12 in. until late in May when they elongated somewhat in response to the shade of the rapidly developing grass. Altogether they occupied only a small part of the soil surface.

Species of the prevernal aspect are all relatively shallow-rooted perennials. All are of low stature and blossom and ripen their seeds rapidly in an area which is well lighted for only a few weeks in spring. Flowering of some may continue into May. Plants of some species then disappear above ground; others linger on in the dim light of the understory.

In the early days of May the prairie changes in appearance from that of winter. Big bluestem is 1-3 in. high and its new green soon obscures the bases of the old stems. Although canada wild-rye and switchgrass were 6-8 in. tall, they were not abundant, and there were not enough forbs, except locally, to relieve entirely the drab aspect of winter. All vegetation was now growing rapidly; big bluestem during May grew at the rate of 0.5 in. per day, and by the end of the month its shoots had about 6 leaves and a general foliage height of 16-18 in.

The numerous forbs of the vernal aspect developed so rapidly and attained such heights that they completed flowering before they were overtopped by big bluestem or other tall grasses. Moreover, the summer-blooming forbs grew so rapidly that nearly all equaled or exceeded the grasses in height. Forbs blooming in autumn stood out conspicuously above the grasses.

The last week in May witnessed the completion of blossoming of most vernal forbs. The landscape was rapidly redecorated with species and societies of summer.

At the beginning of the summer aspect the tall grasses had attained a height of at least 16 in. Forbs had extended upward even more rapidly and thus maintained a place in the light. The summer bloomers were gradually overshadowed by the foliage of the grass which by mid-July reached a general level of 2.5-3 ft. But willow aster and tall goldenrod, both autumnal bloomers, extended upward from 2 ft on June 1 to 4 ft in mid-July, and saw-tooth sunflower from 3 to nearly 9 ft.

Late in July the appearance of the prairie gradually changes. The bluestem foliage has now almost completed its development, and forms a deep cover 2.5-3 ft thick. Thus, the average rate of growth was more than 0.5 in. per day. The great mass of vegetation had a profound effect on modifying the amount of water of soil and air, wind, and light. Despite the large amounts of water daily transpired, the soil remained well supplied except during the most severe years of drought. Even in the surface foot 5-15% was nearly always available for growth, and at greater depths to 6 ft, 15-20%. These conditions were ascertained by weekly soil sampling in various prairies over a period of several growing seasons. The still deeper soil was also well moist.

Average day humidity during drier growing seasons (but not in drought) was about 50-65% and during moist ones 60-95%. These data are from self recording instruments placed at a height of about 6 in. in undisturbed big bluestem prairies. Relative humidity was almost always higher near the soil surface than in or above the foliage of the grass. But even above the foliage at noonday, humidity was often 50%. Midsummer determinations near noonday at a height of 1.5 ft, for example, gave readings 8 to 15% higher than at 3 ft. Near the soil surface the humidity was further increased 3-8%. Wind near the soil surface, after the vegetation had established a complete cover, was almost nil. Late in summer only 2-5% as much air movement as that above the vegetation occurred at 2-3 ft in height.

Light was the chief limiting factor to plant development. The forbs of early spring always remained near the surface of the soil where for a time they received full sunlight. At the beginning of the vernal aspect the grass was only 2-3 in. high. Thus, during the long days of May the new crop of forbs was at first well lighted. Moreover, these plants grew somewhat taller than the prevernal ones; hence their competition for light was not severe. But with the rapid growth of the bluestem, light at 12 in. height was reduced to 15-20% of full sunshine, and near the soil surface to only 3-5%. As the season progressed, light in the understory became progressively less.

It is during the autumnal aspect, in August and September, that blossoming of big bluestem reaches its maximum. At this time the flower stalks stand 4-5 ft above the foliage level of early July. When examined in September, a lateral view of the prairie clearly exhibits its layered structure. This is beautifully shown during the process of mowing. Plants, or their dried remains, of most of the prevenal species may be seen as well as those of the vernal aspect. Plants of this lower layer scarcely extend to heights greater than 8-16 in., and the layer is by no means continuous.

A middle layer, which is much more prominent, occurs at a height of 1.5 to about 3 ft. The great mass of vegetation in the upper layer of forbs consists of rosinweeds, sunflowers, asters, goldenrods and other coarse plants of the autumnal aspect. These vary in height from 4-15 ft.

These layers of forbs by themselves, however, do not constitute the vegetation. By full adjustment in time and place, nature produces these varied species in a framework of grasses so dense that one penetrates it on foot with difficulty, and so tall that one might easily become lost in the maturing vegetation of a single growing season.

Thus, the vegetation changes from a simple open structure of early spring to a more complex one with a middle layer as it grows higher with the progress of the season. Finally, with the development of an upper layer of forbs, and the lengthening of the flower stalks of grasses, mostly in late summer and autumn, a very complex structure results. Throughout the three major aspects the controlling vegetation is big bluestem. The habitat usually supplied excess of factors for growth-water, nutrients, light and heat-after the demands of the dominants had been met. The intensive utilization of these factors is possible because of the plan of life in the prairie is so diverse. As the season advances there is a constant shifting and readjusting as the component species of higher layers continue to develop and increase their stature.

Early in September of a normal season the green color of big bluestem, indian grass, and switchgrass is slowly replaced by the red and bronze and golden tints of autumn. As the season progresses these colors gradually deepen until the landscape presents a color scheme of exquisite beauty and delicacy of painting. But before this time is reached, ordinarily comes the mower. This tremendously varied and intermixed crop is harvested and only the stubble, like that of the preceding spring, remains. But this is essential to maintain prairie as it has been described; the rebuilding will begin once more come spring. If the mass of dead plants is not removed by havmaking or fire, or kept from accumulating by grazing animals, the grassland as described will deteriorate after several years and become quite unlike that known to the original white owners, which condition has been faithfully described (Weaver & Rowland 1952).

SUMMARY

A long-time study has been made of the origin and development of streams in prairie and the woodland vegetation which often borders them. Contacts of the woodland with prairie have been described. The area examined extended about 350 mi along the axis of the Missouri River and from the Mississippi-Missouri divide in Iowa westward about 200 mi to the edge of the Great Plains. Special consideration was given to the development of the bluff-rimmed flood plain of the Missouri and other large rivers.

Most of the 23-34 in. of rainfall is absorbed by the deep, granular prairie soil, but following heavy rains or rapidly melting snow on frozen soil, water from converging slopes flows downward into ravines. At first the course of the headwater is marked only by a more luxuriant growth of grasses and forbs, but as the intermittent stream cuts into sod to form a channel, wind-blown seeds of various species of willows (Salix) and cottonwood (Populus) produce the first woody vegetation. Joined by other branches, some of which are spring-fed, a channel several feet wide and deep is formed in the course of a few miles and the stream is no longer intermittent. Ash (Fraxi-

nus), boxelder (Acer) and elm (Ulmus), all from wind-blown seeds, become scattered along the banks. Several species of xeric shrubs and vines with fleshy, bird-carried fruits appear. Farther down-stream a flood plain is developed on which hackberry (Celtis), walnut (Juglans) and other trees and an ever increasing number of shrubs and woody vines thrive after migrating upstream from the deciduous forest along the bluffs of the Missouri between Nebraska and Kansas and Missouri. Where sheltering hills or deep canyons occur, a woodland of bur oak may occupy the sheltered slopes but contacts prairie on its upper margin. Unless well protected the upper flood plain may remain as prairie.

Where more mesic forests of red oak, hickory and linden occur in the southeast they extend from the outer edge of the flood plain upward along the bluffs. The bur oak occupies the uppermost slopes or hilltops and contact with grassland is usually, but not always, through hazel (*Corylus*), sumac (*Rhus*), coralberry (*Symphoricarpes*) and other shrubs in a belt of a few feet to 0.5 mi in width.

The larger bottom lands, their development, soils, and vegetation, have been described. The flood plain of the Missouri River is 0.5-1.5 mi wide between South Dakota and Nebraska but 8-15 mi wide southward. A river makes not only its own bed and channel but also fashions the valley through which it flows. The secular shifting of great river channels is recorded in the conformation of the plain. The Missouri is more than 1/4 mi wide where it begins to bound Nebraska and the bluffs bordering the valley are about 140 ft high. It borders Nebraska for a distance of 350 mi but because of its sinuous course the actual length is approximately 500 mi. The river's gradient along this portion of its course is about 1 ft/mi; southward the wooded bordering bluffs may extend upward 250 ft above the flood plain.

The first bottom land of the flood plain is an expression of former channels of the river and materials which they constructed. Soils of the mixed alluvial land formed from recently deposited sediments lack distinct horizons. They vary from heavy clays, heavy clays over silt and sand, loams and silt over sand, to coarse sand. They usually occur near the river channel and are subject to occasional or frequent flooding. These soils, sometimes covering 40% of the plain, are occupied partly by trees, mostly willows and cottonwood, shrubs, sedges and rushes, and, in part, by various hydric grasses.

Topography of the second bottom land, which is often 10 or more feet higher, may result from the leveling processes of sedimentation by slack water from the river's flooding. Drainage out of the hills is mainly that of many small streams, often fed by numerous springs, that do not cross the flood plain but fill the ponds and lakes with sediments from the upland. Second bottoms of the Missouri and other large streams present poorly drained clays and silty clay loams. The poorly drained wet meadow soil occurs mostly on the wider and flatter parts of the flood plain, usually near the bluffs. On the wet

meadow soils prairie cordgrass (Spartina), switchgrass (Panicum) and wild-rye (Elymus) thrive. On Brunizem (prairie) soils of silt loams and clay loams, occupying the higher parts of the upper flood plain and mostly well drained, vast prairies of big bluestem are found. Second bottom soils are rarely flooded. Topography of the flood plain, names and locations of the various soil types, and their relation to flooding are clearly shown by means of drawings.

Flood plain forest consists mostly of various willows and cottonwood, ranging from the water's edge over natural levees to a distance of $\frac{1}{8}$ to $\frac{1}{2}$ mi, northward, and to somewhat greater distances, with increase in number of species, south of Plattsmouth. They also border abandoned river channels, lakes and ponds, but are mostly confined to first bottom land. They are best developed where protected from drving winds by sheltering bluffs. Sandbar willow is the first to become established on river banks and it thickly populates sandbars. Black and peachleaf willows, 20-40 ft tall, are abundant. Cottonwoods, with trunks 3-6 ft thick, tower upward 60-80 ft. Other flood plain trees, such as those along smaller flood plains, also occur, sometimes abundantly. These forests have been described as well as the undergrowth of shrubs and woody vines.

Vegetation of the numerous swamps and extensive marshes has been described. Bulrushes (*Scirpus*), cattails (*Typha*), reed (*Phragmites*) and bur reed (Sparganium) grew in water 1-8 ft deep in dense stands often extending as far as the eye could see. Marsh vegetation is rooted in waterlogged soil where the water level in summer is close to the soil surface. Chief species were the grasslike sedges 2.5-3 ft high, many of which are pictured and described. Spike rushes (*Eleocharis*), smartweeds (*Polygonum*), water hemlock (*Cicuta*) and many other forbs such as iris and various mints inhabited the marshes. The total area occupied by marshes was very large.

Great areas of the flood plains, intermediate in drainage between the marshes and bluestem prairie, supported continuous grassland of prairie cordgrass. It grew in dense stands from thick rhizomes. The stout stems were clothed with leaves about a half in. in width and 2.5-5 ft long. Foliage height ranged from 5-7 ft and the dense shade often excluded most other plants. Other wet-land grasses were rice cut-grass (*Leersia*), virginia wild-rye (*Elymus*), reed canary grass (*Phalaris*) and redtop (*Agrostis*). Shrubs were often intermixed and also a large group of tall coarse herbs.

Transition from this wet-land vegetation is through narrow to very wide zones dominated by switchgrass, a tall, coarse sod-forming species, and canada wildrye, also a coarse grass but of somewhat lesser stature.

The rapid growth and almost complete dominance of big bluestem on the best drained soils and its possession of the major portion of second bottoms have been discussed. Community life in this prairie, the changing structure of the vegetation with the progress of the season, and the wonderful productivity of the prairie soils have all been considered. This study, begun in 1916, has endeavored to picture the native vegetation in its original condition, as a scientific record of the past. After the turn of the century drainage districts were formed. Lakes and marshes at the margins of the flood plain were filled with soil from the uplands by diverting the water from the hills into them, where the transported soil settled out. Later powerful modern machinery was used in clearing away trees and digging deep drainage ditches. Native vegetation throughout the bottom land, except near the river channel, has been almost completely replaced by farm crops.

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