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REPLACEMENT OF TRUE PRAIRIE BY MIXED PRAIRIE IN EASTERN NEBRASKA AND KANSAS¹

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Destruction of a portion of one plant association and its replacement by another has just been completed. This has occurred not as the result of man's interference with the vegetation nor the effect of his grazing animals. It has been due to a dry climatic cyle and has been accomplished within a period of seven years. The scene of action was the broad area on the western edge of true prairie in central Kansas, eastern Nebraska, and eastern South Dakota. It is distinctly east of the mixed prairie in the central portion of these states. Although the phenomenon was general over hundreds of square miles of grassland, it has been studied in detail from year to year in only a few widely separated places. Three of these have been selected to illustrate this remarkable transition in grassland populations and structure and the manner in which it occurred, as well as the time relations and the causal factors.

True prairie is characterized by a continuous stand of certain dominant grasses of medium stature—mid grasses. Although there is an under layer of forbs with a few low-growing grasses, these form open stands, are not continuous, and are distinctly subdominant. Hence, true prairie is readily distinguishable both in physiognomy and structure from mixed prairie with its dominant mid grasses and dominant short grasses. These typically form an upper story and a lower layer respectively, or short grasses of the drier places may alternate with the mid grasses of less xeric sites. In addition, the eudominants of the two associations are, of course, different, and even the perdominants exhibit differences in appearance, in size, and often in habits of growth in the two associations (cf. Clements and Shelford, '39).

SAMPLE PRAIRIES

The three prairies selected for illustration had been studied at two periods just before the drought and intensively summer after summer following 1934. They are located, respectively, 65 miles southwest of Lincoln near Carleton, Nebraska; 30 miles northwest of Carleton near Clay Center, and 45 miles southwest of Carleton near Montrose, Kansas. These bluestem prairies were ungrazed but mowed in fall for the crop of hay. They were entirely representative of the area as a whole, considerable parts of which are still unbroken prairie and pasture land. They are in the Chernozem zonal or climatic soil group.

The Carleton tract is a nearly level upland prairie formerly 80 acres in extent, with a broad shallow ravine running its entire length. The soil is Crete silt loam and, like the following soils, is described by Robertson ('39): "The topsoil is dark brown to black and coarsely

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granular. Lime is generally present at a depth of 2 to 3 feet and the soil is brown to light brown, hard, and rather impervious at this depth. In the swale in the wheat-grass type a definite claypan is present beginning at 9 to 12 inches and extending to depths of 26 to 30 inches. Over the remainder of the prairie this layer is present but more pervious and less superficial."

The grassland at Clay Center is a welldrained unbroken tract, formerly of about 20 acres, crossed by a shallow swale. The soil is Hastings silt loam. "It is readily penetrable by water and roots and has the lime layer at a depth of over 4 feet. This type is considered excellent for corn and is almost entirely under cultivation in Clay County."

The Montrose prairie consisted of 60 acres of moderately rolling land with some nearly level areas and shallow ravines. "The soil in the ravine is Lincoln silt loam, colluvial phase; that of the slopes is Colby silty clay loam. The 6-inch layer of eroded topsoil is a dark, pervious mantle of silt loam underlain by a subsoil consisting of about 20 inches of grayish to light brown, slightly compacted silty clay loam above unweathered loess."

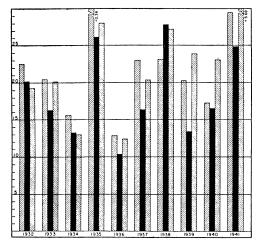


FIG. 1. Annual precipitation in inches near the prairies at Clay Center (black), Carleton (diagonal lines at left), and Montrose (diagonal lines at right) from 1932 to 1941 inclusive.

DROUGHT AND CHANGES IN VEGETATION

The normal precipitation is 27.3 inches near Carleton, 25.5 at Clay Center, and 25.0 inches near Montrose. Annual precipitation at these stations is given for two predrought years, the extremely dry years of 1934 and 1936, and the remaining years until the drought was definitely broken in 1941–42 (figure 1).

The broad outlines of the changes in the vegetation year by year that resulted in mixed prairie are as follows:

- 1932–33 Predrought bluestem prairie
- 1934 Great deterioration
- 1935 Western wheat grass spread widely
- 1936–37 Further losses; wheat grass increased
- 1938 Wheat grass and short grasses increased; revival of relicts
- 1939 Side-oats grama increased greatly and competed successfully with wheat grass; short grasses increased
- 1940 Great losses of prairie relicts and side-oats grama; wheat grass and short grasses possessed the prairie
- 1941 Mixed wheat grass—short grass prairie

The terrific impact of the drought in 1934 has been described (Weaver, Stoddart, and Noll, '35). Likewise the results during the following year (1935) in Iowa, Nebraska, and Kansas have been fully presented (Weaver and Albertson, '36). The results of intensive field work in these and adjacent prairies during 1936 and 1937 have been fully described by Robertson ('39). Further studies on the progress of the recovery of vegetation from drought over a wide area until 1939 have been reported (Weaver and Albertson '39, '40, '40a).

Numerous other researches reveal not only the great intensity of the drought but also the very large area of grassland



FIG. 2. View in Carleton prairie in spring, 1940. The shallow swale in the foreground (light color) is occupied mostly by relict big bluestem. Western wheat grass (dark color) occupies three-fourths of the prairie. It is 8 inches tall, and extends beyond the haystack for a quarter of a mile. The bluestem area is being invaded by wheat grass.

bluestem area is being invaded by wheat grass. FIG. 3. Relict bunches of big bluestem that have recovered from burial by 2 to 4 inches of windblown soil. They are completely surrounded by western wheat grass which invaded this area and caused dwarfing and death of most of the bluestem by 1940. Photo June 23, 1938. affected by it (Albertson, '38, '39, '41; Albertson and Weaver, '42, '43; Allred, '35, '41; Beath, '35; Bell, '35; Ellison and Woolfolk, '37; Gates, '34; Pechanec *et al.*, '37; Savage, '37; Savage and Jacobson, '35).

Record of Change

The history of the major changes in these prairies is reported briefly and somewhat schematically. Changes in the three prairies may be directly compared by reading each year's story from left to right. The history of an individual prairie may be obtained by reading down the column. The fate of the vanishing dominants is set out in blackfaced type, and that of the widely spreading western wheat grass in italics. Hence, either may be followed without reference to the other vegetation. Perennial grasses involved are little bluestem (Andropogon scoparius), big bluestem (A. furcatus), blue grama (Bouteloua gracilis), side-oats grama (B. curtipendula), buffalo grass (Buchloe dactyloides), western wheat grass (Agropyron smithii), and Scribner's panic grass (Panicum scribnerianum). In addition are the annual sixweeks fescue (Festuca octoflora), downy bromegrass (Bromus tectorum), and Japanese bromegrass (B. japonicus).

BEHAVIOR OF OTHER SPECIES

Indian grass (Sorghastrum nutans) completely disappeared at all three stations after the initial years of the drought. Little bluestem entirely disappeared from Clay Center, it was practically exterminated at Montrose, and only poorly represented in the best preserved fragments of predrought prairie at Carleton. June grass (Koeleria cristata) never survived under western wheat grass; it was of minor importance elsewhere at Carleton, and rare at the other stations. Tall dropseed (Sporobolus asper) was rare at Clay Center but became increasingly common at the other stations. Kentucky bluegrass (Poa pratensis), which

CARLETON

Little bluestem furnished 50 to 85% of cover; big bluestem 50% on lowlands but 20% elsewhere. Mixed bluestem type. A few small areas of blue grama and buffalo grass. Wheat grass was nearly confined to ravines, forming 25-33% of cover locally. Weeds absent; 35 species of perennial forbs.

Little bluestem suffered 95% loss; big bluestem lost 10 to 15%. Less than 1/4 of prairie was covered with a greatly thinned stand of bluestem; 1/4 was mixed (mostly big) bluestems and wheat grass; 1/2 was dominated by alternes of nearly pure but open sod of wheat grass. Both short grasses had increased. Sixweeks fescue was abundant in bared places. Large bared areas were occupied by uniform stands of manyflowered aster. Many dead forbs.

Some growth in spring; all grasses dried in July. **Further death of bluestems by drought.** More forbs died. Aster very abundant locally. Ruderals moderately abundant.

Big bluestem dominant only in local but clearly defined patches. Wheat grass greatly extended its territory (fig. 2). Side-oats grama increased in abundance. Short grasses extended their local areas and started new ones. Aster greatly decreased. Sixweeks fescue and downy bromegrass were abundant.

Big bluestem remained uninvaded in patches 2 x 3 rods or less in area; one alterne in ravine 5 x 8 rods. It had become less important in the fourth of the prairie where it was intermixed with wheat grass. Death of relict vegetation resulted in more extensive areas of wheat grass. It had spread over 9/10 of the prairie. Blue grama increased greatly, patches 1 to 225 sq. yds. in area. Bunches common under wheat grass. Side-oats grama was widely spread in big bluestem areas; it often replaced big bluestem in wheat grass mixture. Buffalo grass increased. Aster greatly decreased as wheat grass spread. Pattern of remaining bare soil shown by dense growth of sixweeks fescue, or small alternes of downy bromegrass. Forbs few, dwarfed.

CLAY CENTER

1932-33

MODERATE PRECIPITATION

Little bluestem constituted 75 to 95% of cover; big bluestem 50% in ravines but 5-20% elsewhere. Mixed bluestem type. A few isolated stalks of wheat grass. Short grasses were common on dry slopes as alternes or mixtures. 35 species of forbs. No weeds present.

1934, Extreme Drought

EXAMINED IN 1935, NORMAL PRECIPITATION

A part of vegetation was buried under 1 to 6 inches of dust; whole prairie dusted. Little bluestem was all dead. Big bluestem persisted mostly in isolated patches, damage heavy (fig. 3). Short grasses, where not buried deeply, were thriving. Sixweeks fescue was densely aggregated in patches on drought-bared soil. Aster had increased. Wheat grass occurred in thin stands on dust-covered soil but as great alternes in driest places; densely aggregated on low ground. Ruderals abundant almost throughout.

1936

MOIST SPRING, DRY SUMMER

Continued losses of big bluestem and most grasses. Wheat grass grew in nearly pure stands where it invaded earlier, and in widely spread thin ones. More forbs died. Weeds abundant; dense patches of downy and Japanese bromegrass.

1937

MOIST SPRING, DRY SUMMER

Big bluestem and most predrought grasses suffered further losses. Wheat grass had spread over most of the prairie. Blue grama bunches occurred widely. Enormous crop of weeds dried in June. Annual bromegrasses dominated much of the lower land.

1938

NORMAL PRECIPITATION

Prairie weedy; wheat grass covered 3/5 of it, more than half being a nearly pure stand, the rest with an understory of bunches of blue grama (fig. 4). Next largest type was annual weeds on areas repeatedly dusted, last time in 1936. Pure open stands of blue grama were third in area occupied. Very little side-oats grama. A few small patches of big bluestem remained and widely scattered isolated plants of big bluestem and other grasses were thriving among weeds. Some nearly pure patches of Pennsylvania sedge. Scribner's panic grass was prominent in pure local stands. Patches of annual bromegrasses suppressed widely scattered perennials. Forbs were much reduced, especially under wheat grass. Aster was the chief weedy forb.

MONTROSE

Little bluestem composed 65 to 80% of cover; big bluestem 98% on lowlands but 5-20%on uplands. Mixed bluestem type. Side-oats grama often composed 10-15% of cover. Wheat grass occurred mostly as isolated plants; occasional clump of short grass. 44 species of forbs. No weeds.

Little bluestem was reduced to 1%; losses of big bluestem were very severe, only local patches left. In many places 75% of vegetation had died, and even 50% on low ground. Often open stands of big bluestem alone remained. Only 1/3 to 1/5 of basal cover was left. Short grasses lost least and were spreading rapidly. Wheat grass stands had appeared, especially in dusted places. Many dead forbs. Abundant potential weed population.

Fair growth in spring; wheat grass invaded dustcovered areas forming open cover; also patches in ravine. All grasses dried in July; big bluestem and others suffered further losses. Many ruderals.

Big bluestem and most predrought grasses decreased. Wheat grass extended its area. Short grasses increased. Many weeds. Forbs much reduced in numbers and stature.

Prairie a mosaic of types; about 4/10 was pure, flourishing, wheat grass type; 3/10 was covered with wheat grass-side-oats grama mixture, large distinct bunches of side-oats grama formed half of mixture, but sometimes occurred in pure stands. Remaining 3/10 composed of three types: (A) sideoats grama and big bluestem, the latter spreading and sharing space of dead little bluestem with side-oats. This type occurred in patches and streaks. (B) Big bluestem which had spread and formed pure stands in relict patches of bluestem prairie; and (C) blue grama-buffalo grass type well distributed and spreading throughout, also many isolated new stands. Basal cover was still open except under old wheat grass. Sixweeks fescue was abundant. Forbs greatly reduced in species, number, and stature. Annual weeds were scattered sparingly throughout.

CARLETON

Side-oats grama thrived as wheat grass waned; it had invaded or was invading wheat grass nearly over the whole prairie; it was the most important species, wheat grass ranking second. Blue grama and buffalo grass were still increasing. Pure wheat grass stands were greatly thinned by invasion of side-oats grama and short grasses, or wheat grass was thinly invading short grasses and thus forming mixed prairie (\tilde{ng} . 5). But pure short-grass stands were common. Many equal mixtures of big bluestem and side-oats grama. Also many small pure stands of side-oats grama. Pure big bluestem had thickened its stand but size of areas had decreased. Basal cover in general greatly increased, soil mulch reappeared, much less bare ground, weeds few, except bromegrasses in patches. Very little aster. Forbs almost rare.

Much big bluestem had died. Many former mixed patches were now all wheat grass. Largest relict area maintained many prairie species, even little bluestem. All but 1% of side-oats grama had died, forming an open lightcolored layer under wheat grass. An exception was 5% left in ravines. Some recovery in fall. Wheat grass increased greatly; occupied 3/4 of prairie. Stand was thicker, better cover of debris. Blue grama and buffalo grass increased greatly. Practically no weeds, except large patches of bromegrass. Forbs reduced to 19 species, scarce. No aster, all of its area was occupied, mostly by wheat grass. Total yield 0.45 ton per acre.

Big bluestem had decreased. Periphery of big bluestem alternes invaded 6 to 10 ft. by wheat grass. Wheat grass thickened old stands everywhere, occupied all bare soil, and established thin new growth throughout smaller patches of bromegrass. Also invaded periphery of all larger ones and occurred as small dense patches in them. It had spread into short grasses, especially buffalo grass. This intermingling with and increasing of short grasses had resulted in mixed prairie over 2/5 of entire area. Side-oats grama was present, mostly sparingly, with a few other very minor grasses. Overwhelmingly heavy cover of wheat grass with or without short-grass layer. Total yield 2.43 tons per acre.

CLAY CENTER

1939

Dry Early, Moist in Late Spring, Dry Summer

Big bluestem had not increased, injured by drought. Flourishing side-oats was scattered widely but thinly through wheat grass. Wheat grass was doing poorly, it had increased its areas somewhat but stands were often unconsolidated. Bunches of blue grama were scattered widely; it controlled about 1/3 of the prairie; often formed an understory to wheat grass (fig. 6). Carex formed two large nearly pure areas. Some large, half-bare areas were being revegetated by mixed perennial grasses, including wheat grass. Scribner's panic grass was abundant. Weeds few, dwarfed. Bromegrass was much reduced, permitting fair growth of perennial relicts. Species of grasses and forbs few.

1940

DRY TO MOIST SPRING, DRY SUMMER

Big bluestem greatly weakened or dead. Wheat grass had invaded the few, small relict patches on all sides, occupied much bare soil in thin stands, and was encroaching on edges of other alternes. Much of wheat grass was of open growth and weed infested. Considerable open ground in which various relict and invading grasses competed with coarse weeds. Sedge increased. Much side-oats grama had died. Some blue grama died, increased in general, stands open. Bromegrasses thick in their alternes where isolated relict grasses succumbed. A weedy prairie. Forbs reduced to 24 species. Total yield 0.62 ton per acre.

DROUGHT ENDS

1941

WET SPRING, MODERATELY MOIST SUMMER

Drought losses heavy; 95% of remaining big bluestem and nearly all other relict grasses killed. Much side-oats grama, Carex, and even some blue grama died. Wheat grass was less vigorous but had spread more widely. Except for wheat grass and blue grama, vegetation was composed of annual weeds; 1/3 was weeds or with only a thin growth of wheat grass; no weeds occurred in dense stands of wheat grass. Bromegrass was dense in its alternes, perennial relicts dead or dormant. Here wheat grass was slowly invading. Total yield 2.38 tons per acre. (In 1942 a good wheat grass—short grass prairie was established.)

MONTROSE

Wheat grass had spread greatly, rhizomes threaded through much big bluestem and side-oats grama territory, thus entering the most mesic sites. Side-oats grama ranked second in importance and was in better condition than wheat grass in this mixture. Big bluestem was not increasing; it ranked third and was handicapped by drought. Broad alterne on mid-slope reduced to 30 feet in width. Both short grasses thickened and extended old areas and established many new ones, often under wheat grass. Forbs rare, some dying. Drought severe, half of prairie burned in July.

Big bluestem greatly reduced by drought; relicts small and few; largest alterne had shrunk to 3 to 18 feet in width and a few rods in length. Side-oats grama sparse, not thriving. Short grasses increased greatly with new centers of growth almost throughout; often intermixed with wheat grass. Wheat grass flourished in spring, thickened old stands, spread everywhere, and replaced nearly all relict big bluestem on north slopes and in ravines. Overwhelmingly wheat grass or wheat grass-short grass prairie. Other grasses less than 3%. Total yield 0.61 ton per acre. Forbs reduced to 21 species.

Big bluestem nearly gone; largest alterne now fragmented, greatest width 10 feet. Wheat grass was scattered throughout the largest big bluestem alterne. Side-oats grama generally decreased, some revived. Short grasses increased rapidly; as in other prairies, blue grama exceeded buffalo grass by 1/2 to 2/3 in amount. Wheat grass occupied nearly the whole prairie with or without a layer of short grasses. Debris accumulated. Weeds rare. Total yield 2.78 tons per acre. occurred sparingly in two prairies and in abundance of 10 to 15 per cent locally at Carleton, was not found at the end of the drought, except very sparingly under the relict big bluestem at Carleton. Sand dropseed (*Sporobolus cryptandrus*) entered the prairies after 1934. It was scattered sparingly, aggregated in a few areas locally, and survived the severest drought. Scribner's panic grass occurred sparingly in relict areas at Carleton, in one ravine only at Montrose, but became an important pioneer in low, dust-deposited soil at Clay Center. There was only a little Carex pennsylvanica at Montrose; it exhibited good resistance to drought and increased at Carleton, and developed numerous large dense patches at Clay Center, but declined there near the end of the drought.

Sixweeks fescue was not important at Clay Center, except in 1935; it was scattered lightly in all grass types, but especially in and about short grasses at Montrose. It played its usual important role as an early occupant of bare soil at Carleton. Little barley (Hordeum pusillum) was sparse at Montrose, never occurred in quantity at Clay Center, but became abundant in the wheat grass at Carleton. It bulked small, however, compared with its abundance of 1 to 2 tons per acre in the degenerated mixed prairie farther westward (Weaver and Mueller, '42; Albertson and Weaver, '43). Bromegrasses were not common at Montrose but played a prominent part in the subsere at the other stations where dense stands occurred. They utilized large amounts of water, and produced deep shade both when alive and after they had dried and lodged. But they were gradually replaced by western wheat grass and short grasses. Weeds occurred only sparingly in wheat grass, except at Clay Center where they were frequently abundant, especially in 1940. They were, in addition to the weedy grasses, chiefly Lepidium densiflorum, Chenopodium album, C. leptophyllum, and dwarfed Salsola pestifer. These



FIG. 4. A pure heavy stand of western wheat grass on low ground on July 15, 1938. The lodged plants form a cover 5 to 8 inches thick. This area at Clay Center was formerly occupied by big bluestem.

FIG. 5. A thin stand of western wheat grass which has recently invaded an area already occupied by buffalo grass and blue grama. Photo of this mixed prairie at Carleton, August 11, 1939.



FIG. 6. Various stages in development from seedlings to 3-year-old bunches of blue grama. The 14 plants were obtained in 1939 from a wheat-grass area of four square meters at Clay Center. They represent the early development of the lower layer in mixed prairie.

species also occurred in bared areas especially at Clay Center, but to a less extent at Montrose, being fewest, except bromegrasses, at Carleton. Other important species were *Leptilon canadense*, *Panicum capillare*, *Amaranthus retroflexus*, and *Helianthus annuus*. Weeds were nearly all finally replaced by western wheat grass or short grasses.

Forbs that entirely disappeared included Meriolix serrulata. Psoralea argophylla, Salvia pitcheri, and Liatris scariosa. Even plants of Amorpha canescens, Rosa arkansana, and Kuhnia glutinosa died during 1939. Amorpha canescens was the only species of perennial forb that persisted well under wheat grass. Two forbs became common at all stations after 1936 and increased year by year until they became very widely distributed and usually extremely abundant. They were Oxalis violacea and Anemone caroliniana. Both have relatively large organs for food accumulation, bulbs and tuberous rootstocks respectively, and both blossom and produce seed relatively early in the growing season (cf. Resurvey of forbs. Weaver and Albertson, '43).

DISCUSSION

A good development of western wheat grass is dependent upon sufficient available soil moisture in spring and early summer. This grass is of northern extraction and renews activity in this area usually in March. It develops rapidly in April and May, often attaining full vegetative stature and producing flower stalks early in June. Since there was usually little reserve water in the soil during the drought years, growth of wheat grass was nearly always dependent upon spring rainfall (Weaver, '42).

Precipitation from March to May inclusive in 1934, together with water reserves at the beginning of this extremely dry year, seem to have been sufficient to promote a good growth of wheat grass (figure 7). Enough precipitation occurred during this period in 1935, when

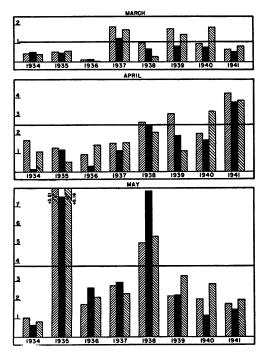


FIG. 7. Precipitation in inches in March, April, and May (1934 to 1941) near the prairies at Clay Center (black), Carleton (diagonal lines at left), and Montrose (diagonal lines at right). Average normal monthly precipitation at the three stations (from which any station varied but little) is indicated by a heavy horizontal line.

competition for water was greatly reduced by death of more mesic grasses, so that the spread of wheat grass was very great. There was a reserve of moisture in the soil following 1935 which coupled with moderate spring rainfall in 1936 promoted its continued spread. Conversely, the low summer rainfall, dry soil, and other conditions of growth were extremely detrimental to later developing grasses. Clay Center, for example, had only 40 per cent of the normal precipitation. A period of drought beginning on June 5 extended for 24 days without rain. A shower of .56 inch then fell but was followed by 37 days with no effective rainfall. Robertson ('39) describes conditions at Carleton as follows: "Four days spent on this prairie in the middle of July, 1936, served to impress one with the severity of physical and biotic factors so extreme that even native vegetation could not endure them uninjured. Daily maximum temperatures ranging from 104° to 111° F. accompanied by relative humidities of 19 to 24 per cent, continuous strong winds, glaring sunlight, and subnormal precipitation combined to make the grasses crackle underfoot like wheat stubble. Only false prairie boneset (*Kuhnia glutinosa*) and blazing star (*Liatris punctata*) appeared unhampered by drought, and they were borne down and partly eaten by hordes of grasshoppers."

In 1937 the moist spring was very favorable to an excellent development of wheat grass. It greatly extended its territory in all of the prairies. Big bluestem, however, already weakened by the previous summer's drought, suffered further losses during the dry summer.

A year of good precipitation, 1938, accelerated the spread of wheat grass. Its dominance was extended even more widely. Side-oats grama which had in-

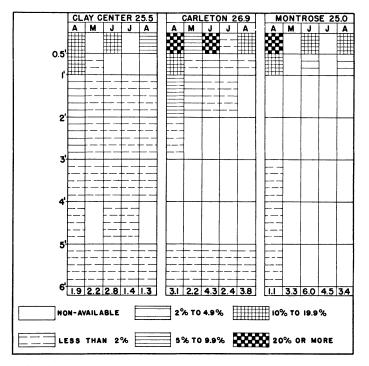


FIG. 8. Available soil moisture to a depth of 6 feet at three wheat-grass stations in 1939. Normal precipitation at each station follows the name, and total current monthly rainfall is given at the foot of each column.

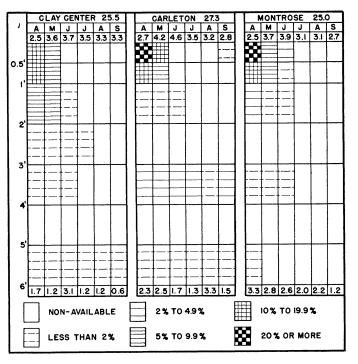


FIG. 9. Available soil moisture to a depth of 6 feet in 1940. Normal'annual precipitation at each station follows the name, normal monthly precipitation is below the letter indicating the month, and current monthly rainfall is given at the foot of each column.

creased greatly, distinctly profited also, often by utilizing the space left bare by the death of big bluestem. Vigorous bunches 3 to 6 inches in basal diameter with flower stalks 3.5 feet tall were scattered widely and seed was produced in abundance. There was much bare soil in the aggregate open for colonization. Even big bluestem increased its area locally.

Wheat grass waned in 1939, perhaps in part because of its remarkable growth and seed production the preceding year but partly because of severe competition with an enormous stand of side-oats grama. This occurred following a spring during which the soil was at first dry but later became moist. Summer was dry (figure 8). Although the wheat grass did not produce heads (except where it grew without competition on newly deposited soil) it survived the very dry summer as did the most xeric grasses —blue grama, buffalo grass, and sideoats grama. Finally all of the grasses dried and all green color disappeared from the landscape except that of an occasional deeply rooted forb as *Kuhnia*, *Amorpha*, or *Rosa arkansana*. At Clay Center the vegetation was so dry and drab that it appeared as if it had been frosted.

Wheat grass made good gains in territory during the moderately favorable spring of 1940. Its former competitor, side-oats grama, suffered enormous losses. Disease played an important part (Fowler and Weaver, '40) but death was due also to unfavorable environment (figure 9). Summer was so dry that late in July the remaining big bluestem was mostly dead above ground and reddish brown as is usual in late autumn. Wheat grass was a light tan in color. The vegetation crunched underfoot and would have burned readily. Drought was most extreme at Clay Center where even some blue grama died and where death and deep dormancy delayed recovery in 1941.

The excellent growing season of 1941 (figure 10) permitted wheat grass to complete its dominance in the upper (mid grass) layer. Its heavy foliage and abundant spikes were very impressive. The short grasses had spread slowly to rapidly from year to year almost without interruption and now formed the understory or occurred in the usual small to large patches and alternes characteristic of mixed prairie.

The formation of mixed prairie became clearly apparent in 1938 when an intermixing of wheat grass and short grasses along their numerous ecotones became pronounced. Tufts and small patches of buffalo grass, often on the lower ground, had become common under wheat grass while, usually on the higher land, blue grama was similarly widely scattered in bunches and patches everywhere. Its seedlings survived during periods in the drought years so unfavorable that all others succumbed. Mutual invasion of short grasses and wheat grass progressed in the spring of 1939. It was delayed somewhat at Clay Center by extreme drought in 1940 but became more marked elsewhere. The process was nearly completed over much or most of the prairies at Carleton and Montrose in 1941, but not until 1942 was a good mixed prairie established at Clav Center. In certain other prairies the transition has not yet been completed, patches of true prairie still remaining intact.

The formation of mixed prairie has oc-

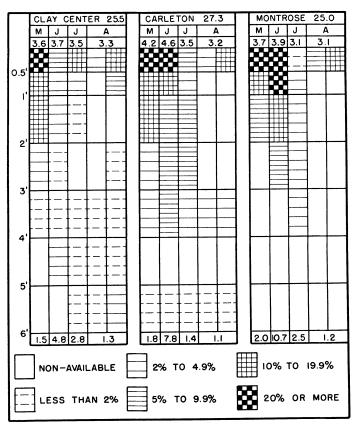


FIG. 10. Normal annual and normal monthly precipitation, current monthly rainfall, and available soil moisture at the Nebraska-Kansas wheat-grass stations in 1941.

curred in the western edge of true prairie throughout a belt 100 to 150 miles in width. Western wheat grass was formerly present in much trampled portions of native pastures and in small amounts along fences. It has swept through pastures as well as prairies with astounding rapidity since 1934. It has often taken nearly complete possession of extensive pastures and ranges (Weaver, '42). This has been accomplished both by wind-blown and rodent-distributed seed and by extensive propagation by long, slender, much branched rhizomes. The rhizomes advanced several feet a year and produced an abundance of new stems, frequently 1000 to 1300 per square meter.

Short grass pastures along the western margin of true prairie have very greatly increased during drought in numbers and in total area. They extend eastward beyond the Big Sioux river in South Dakota and to within 40 miles of the Missouri river in southern Nebraska (Weaver and Hansen, '41). Western wheat grass has become abundant in many of these overgrazed short-grass pastures, especially where stock was excluded for a time. A mixed short grasswheat grass type has been the result.

SUMMARY

The replacement of true prairie by mixed prairie has occurred as a result of drought in an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota. The change of plant populations and structure of vegetation is described in detail as it occurred in three widely separated representative native prairies. Predrought vegetation consisted mostly of little and big bluestem with only small amounts of western wheat grass, side-oats grama, and the short grasses—blue grama and buffalo grass.

The chief dominant, little bluestem, mostly or entirely succumbed to drought in 1934 and 1936. Big bluestem was greatly damaged. It finally nearly disappeared in 1940. Western wheat grass rapidly increased each year. In 1939 it was held in check by an enormous spread and excellent development of side-oats This competitor, however, sufgrama. fered great losses the following year and wheat grass occupied most of the area. A steady increase and wide distribution of the very xeric blue grama, and, in a smaller degree, buffalo grass occurred synchronously with the rise of wheat grass. By mutual invasions of the mid grass and short grasses, typical mixed prairie became clearly apparent in 1938. By 1941, seven years after the drought began, these grasslands were almost entirely transformed into mixed prairie.

Where native true prairie had been weakened by grazing and trampling, or where it had degenerated to short-grass pasture, wheat grass usually gained even earlier entrance and spread with great rapidity, often resulting in a wheat grassshort grass mixed prairie type.

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