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INTRODUCTION

After three years with good precipitation (1941 to 1943), which followed the eight years of drought in the mid-continental grasslands, an extended study was made of the nature and degree of recovery of vegetation (Weaver & Albertson 1944). It was realized at that time that the mosaic of grassland patterns that crystallized out of a mass of recovering vegetation was merely one phase of a long developmental process (Fig. 1). The prairies had suffered a terrible catastrophe. At this time, largely by the tremendous increase of its most drought evading and drought resisting perennial species, mid or true prairie had merely succeeded in repopulating most of the bared soil. Many changes in the plant populations were still to occur. These included the increase of former dominants, then of small abundance; the suppression of drought dominants under the wetter phase of the climatic cycle; the disappearance or reduction to normal numbers of other relicts of drought populations; the increase of drought-depleted forb populations; and a new development of societies.

FIG. 1. A well-drained level lowland near Lincoln, Nebraska, formerly completely covered with big bluestem (*Andropogon furcatus*). Relatively small amounts of this type still remain (foreground). Western wheat grass (*Agropyron smithii*) invaded the drought-bared soil and formed a distinct, pure community (right center), and the needle grass (*Stipa spartea*) type (light) developed in the background. Photo June 10, 1943.

Another necessary adjustment for stabilization was the reduction to the normal level in height of the individual species which, freed temporarily from the community rule of severe competition, grew abnormally and produced an irregular and often patchy type of cover. The re-establishment of the understory in the vegetation and the building of a soil mulch would also mark the return to predrought climax conditions.

These phenomena and numerous others found in the prairie community have now been studied continuously over a period of five years. The same extensive areas in true prairie of known drought and predrought history (Weaver & Fitzpatrick 1934; Weaver & Albertson 1936, 1939, 1940, 1943) have been re-examined many times annually and their development traced in detail by methods of quadrat, transect, and experiment. The study did not extend eastward beyond the Missouri River, for there damage had been slight and readjustment rapid. The environment for development toward stabilization has generally been good and often excellent. The soil moisture relations are reflected in the precipitation which was 35.4, 32.7, and 33.3 inches during three of the four years. In 1946 precipitation was 23.8 inches, which was somewhat below the mean, 27.2 inches; but no prolonged drought occurred. In 1948 precipitation was again high, 30.4 inches.

UPLAND COMMUNITIES PRECEDING AND FOLLOWING THE DROUGHT

The extensive survey by Weaver & Fitzpatrick (1932, 1934) of scores of prairies in the eastern third of Nebraska, the western third of Iowa, and in adjacent areas in South Dakota, Minnesota, Missouri and Kansas, revealed only three prairie types on uplands. In the area surveyed, which was 60,000 square miles in extent, the little bluestem (*Andropogon scoparius*)[1] consociation was not only by far the most extensive community or type but it also occupied a portion of the area many times as great as that dominated by any other species (Fig. 2). In fact, it probably exceeded in area all of the other upland and lowland types combined. Needle grass (*Stipa spartea*) was the chief dominant of a second upland consociation. This bunch grass was of practically no importance in the Kansas and Missouri section and was of minor importance in the entire southeastern portion of the prairie area. But it gradually increased northward where the type became well developed. It covered extensive areas on dry ridges and slopes in the central and northern parts, occuring mostly as broad alternes with little bluestem. A third very minor type but a distinct upland consociation was dominated by prairie drop-

1 Nomenclature of grasses follows Hitchcock's "Manual of the Grasses of the U. S.," that of other species is according to Britton and Brown's "Illustrated Flora," unless other authority is given.

seed (*Sporobolus heterolepis*) (Fig. 3). The areas over which it held control were much less extensive than those of the needle grass type. Various degrees of intermingling of this dominant with needle grass and little bluestem occurred, prairie dropseed often forming 1 to 20 percent of the cover. This community was of such relatively small importance that it held the lowest rank among the six major pre-drought communities of true prairie.

FIG. 2. Detail of little bluestem (*Andropogon scoparius*) community. This species often occurred in nearly pure stands. Note the characteristic bunch habit. Lincoln, July, 1945.

FIG. 3. Portion of a prairie near Lincoln, Nebraska, dominated by a nearly pure stand of prairie dropseed (*Sporobolus heterolepis*). Photo July 10, 1944.

As regards the fate of little bluestem, Weaver & Albertson (1943), in their resurvey of conditions in the prairie at the end of the great drought, state: "Little bluestem, which was formerly the most abundant of all the prairie grasses, suffered the greatest loss. It is now of only intermediate importance and is outranked by six other species. Scarcely a trace remains in half of the 12 prairies closely studied, in others it is rare, and in only portions of two is it abundant. . . . Where the original stands were thinned, they were usually invaded by needle grass, prairie dropseed, blue grama (*Bouteloua gracilis*), or western wheat grass (*Agropyron smithii*), or partially repopulated by a spreading of big bluestem (*Andropogon furcatus*) . . . which formerly accompanied little bluestem."

Small areas of the former little bluestem type where loss of little bluestem was not complete have changed into the relict big bluestem—little bluestem community. Much larger areas are now nearly pure stands of big bluestem. Still others have developed into a type designated as mixed grasses (Table 1).

TABLE 1. Major communities of upland true prairie.

Before the Great Drought (1933)	After the Great Drought (1943)
	OLD OR MODIFIED TYPES
Little bluestem	1. Relict big bluestem-little bluestem (4)[1]
	2. Big bluestem (6)
	3. Mixed grasses (7)
Needle grass	4. Needle grass (3)
Prairie dropseed	5. Prairie dropseed (8)
	NEWLY DEVELOPED TYPES
	6. Western wheat grass (2)
	7. Blue grama (5)
	8. Mixed prairie (1)

[1] Numbers in parentheses indicate the sequence in order of area covered by the several communities, mixed prairie being the largest.

In addition, three distinctly new plant communities have developed over large portions of the drought-swept little bluestem consociation. This story is given in detail by Weaver & Albertson (1944). A brief resume of the origin of each of the eight present-day communities in upland prairie will be given so that the degree of stabilization in these during the several good years following their establishment may be better comprehended.

1. A relict big bluestem—little bluestem type resulted from the modification of a part of the pre-drought little bluestem consociation, but it covered relatively small areas and ranked fourth in size among the present-day (1943) upland communities (Table 1). Usually much little bluestem had died and its place was taken by big bluestem. Some, however, survived as dormant crowns.

2. The big bluestem type on upland resulted from the survival of *Andropogon furcatus* wherever the former little bluestem consociation had lost its chief component, *A. scoparius*. After heavy initial losses, big bluestem survived the drought in the bunch form, but later, unless overwhelmed by western wheat grass, spread to form a sod. Its stands on lowland were often greatly thinned, but it usually replaced its losses and re-established the tall-grass type.

3. Mixed grasses formed a community of variable composition over considerable areas formerly clothed with the little bluestem type where widely scattered plants of different species recovered, reseeded, or in-

vaded at about the same time. Here also big bluestem spread widely or renewed growth from dormant rhizomes and formed mixtures with the various other grasses. These species have merely completed the occupation of bared soil where no other type had gained control. The community is not climax.

4. The stands of needle grass were greatly thinned at the inception of drought. But this species in addition to holding all of its original territory, has spread widely. It has not only claimed much land formerly held by the little bluestem type, but has also repopulated much low ground where big bluestem formerly flourished. For here it found, during the drought years, a dry warm soil, similar to its usual predrought home on the uplands.

5. The stands of prairie dropseed were thinned following the first impact of drought even more greatly than those of needle grass. But this species recovered without loss of territory. Seedlings became established over many acres adjacent to old stands and developed into new bunches. Thus the area occupied by this type was increased enormously.

6. Western wheat grass spread by seed and appeared over a wide territory immediately following 1934; invasion was well advanced by 1938. It was favored by moist springs and dry summers, but often utilized all available moisture and thus caused dwarfing or death of most other vegetation. Relict bluestems were usually replaced by pure stands of western wheat grass.

7. Blue grama often survived where all other grasses died. It spread almost without interruption from 1935 to 1942, and promptly thickened its stands (Fig. 4). Buffalo grass (*Buchloe dactyloides*), less abundant and more greatly harmed by drought than blue grama, increased rapidly.

8. A mixed prairie type was formed by the replacement of bluestems by western wheat grass and short grasses and the later intermingling of this mid grass and the short grasses. This began in 1938 and was completed in 1941. Invasion had ceased, since the remaining area was occupied by other vegetation, but not the intermixing of short grasses and western wheat grass.

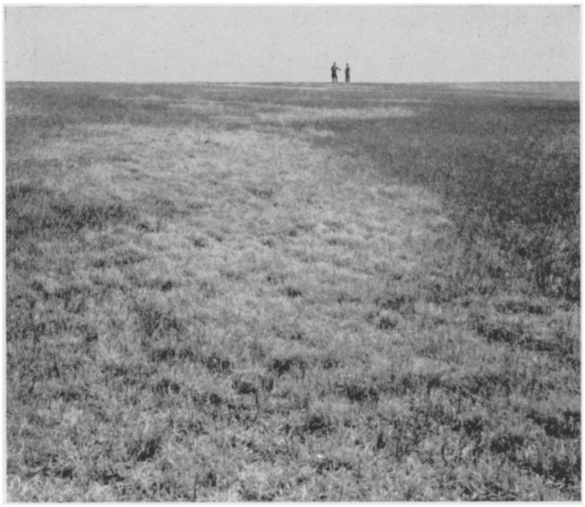

FIG. 4. Invasion of blue grama (*Bouteloua gracilis*) (light) and western wheat grass (dark) on a hillside formerly occupied by the little bluestem type. Hebron, Nebraska.

PERSISTENCE AND EFFECT OF WESTERN WHEAT GRASS

Impressive phenomena in the years following the drought have been the persistence of western wheat grass[2] and the continuation of its marked effect in modifying the water relations of the soil. For despite the fact that it has been largely replaced by big bluestem in parts of a few prairies, in the main wheat grass has persisted. Pure stands are not so abundant as formerly since reciprocal invasions of wheat grass into former areas of short grasses, mostly blue grama, or of short grasses into wheat grass has greatly reduced the area of both these formerly nearly pure types. In many prairies the pure type of either occurs, if at all, only very locally. However, this intermixing resulted not in the re-establishment of true prairie but of mixed prairie instead (Table 1).

Repeated examination of entire prairies, alternes, and numerous large patches completely invaded by wheat grass has shown that this grass has not extended its area since the bared land was claimed by other perennial dominants. Neither has it surrendered its dominance over the areas invaded (with certain exceptions, to big bluestem), although in many places it has shared dominance with blue grama and buffalo grass. A photograph of a rolling upland prairie near Lincoln, Nebraska, at the end of the drought, shows the invasion of wheat grass in seven different places. These appear as dark, very clearly defined patches of vegetation. In the spring of 1947 they were quite as distinct as seven years earlier (Fig. 5). Field studies and comparisons of photographs of various other prairies invaded by wheat grass with conditions in 1946 and 1947 show similar stability (Robertson 1939, Weaver 1944). In the prairie at Hebron, Nebraska, two extensive alternes developed early in the drought, where dust covered large portions of the grassland one-fourth inch to an inch in depth. The largest of these has been examined every year since the development of the stand of wheat grass. In 1947 the area stood out as distinctly as before, the chief change from the original condition being the development of a short-grass layer beneath. Only a very small part remains uninvaded by short grasses. The thick stand of wheat grass is in excellent condition. Big bluestem has advanced irregularly a few feet to a few yards in places along the lowland border. There are few mid grasses present except scattered bunches of purple lovegrass (*Eragrostis spectabilis*) and small amounts

2 Hereafter, for brevity, this species will be designated as wheat grass.

FIG. 5. Portion of a rolling prairie near Lincoln, Nebraska, invaded by western wheat grass in seven distinct places during the great drought. These are the dark patches of vegetation, except the long one in the ravine (foreground) which is Kentucky bluegrass (*Poa pratensis*), an invader on soil washed in from an adjacent field. In this prairie, mowed in autumn, the wheat grass is 5 inches tall; the bluestems have not yet renewed growth. Photo May 2, 1940. Bluegrass invaded this bluestem prairie and greening at the same time as the wheat grass prevented later sharp differentiation in colors.

of tall dropseed (*Sporobolus asper*). A thin, almost continuous layer of hairy chess (*Bromus commutatus*) occurs and keeps the soil fairly well mulched.

DEVELOPMENT OF UNDERSTORY

In the stands that still remain pure or nearly pure wheat grass, the black soil is still only a third to a half covered with plant debris. In places, the drought understory of *Ionoxalis violacea, Hedeoma hispida, Lepidium densiflorum,* etc., prevails. But usually

FIG. 6. A dense stand of hairy chess (*Bromus commutatus*) from a small drought-bared area in climax bluestem prairie in July, 1942. This grass has now almost disappeared except in communities of wheat grass and needle grass where it often forms an understory and later covers the soil with a mulch. In areas of blue grama it is almost always still present as an overstory.

only scattered individuals of these species are found. More often there is an understory, and on good years a very dense one, of hairy chess. This species became abundant throughout the prairies late in the drought. With the return of good rains it almost entirely replaced other weedy brome grasses as *Bromus tectorum* and *B. japonicus* as well as *Festuca octoflora* and *Hordeum pusillum.* It usually grows 10 to 12 inches tall. During its development in early spring and summer, this annual, which often begins growth in the autumn, produces much forage. This dries by midsummer and, lodging in place, forms a good soil mulch (Fig. 6).

Sometimes three distinct layers of vegetation occur where wheat grass is intermixed with short grasses: the short grass has an average height of approximately 6 to 8 inches, hairy chess is 12-14 inches tall, and the wheat grass in head is about 24 to 30 inches high.

CHIEF INVADERS

Aside from blue grama (which ranks first) and to a much lesser extent buffalo grass, the chief native invaders of wheat grass are, in approximate order of abundance, side-oats grama (*Bouteloua curtipendula*) and June grass (*Koeleria cristata*). Tall dropseed, needle grass, and prairie dropseed invade much less frequently; even bluegrass (*Poa pratensis*) invades to a certain degree especially along the eastern and more mesic edge of the range of wheat grass. During the several years of drought the increase and decrease of side-oats grama was periodic. In certain areas and on certain years it was as abundant as the wheat grass. It is believed its present abundance in certain areas of wheat grass is of a similar nature. June grass is of relatively short duration depending more on rapid reseeding than length of life for its place in the grassland. Needle grass and prairie dropseed are far more permanent, but their increase in occupied soil is slow.

COMPETITION IN DROUGHT

A good development of wheat grass, as pointed out elsewhere (Weaver 1943), is dependent upon available soil moisture in spring and early summer. Since there was usually little reserve water in the soil during the years of drought, wheat grass in its early and rapid growth often exhausted all or nearly all of the available supply of water before warm-season prairie grasses and forbs had made much growth. This resulted in the successful competition of wheat grass and in the dwarfing and finally the death of most other species. This dwarfing effect was often pronounced even among the most deeply rooted forbs, plants regularly being reduced to one-half or less of their normal size (Weaver 1942). There was very little competition for light, since even under a good stand of wheat grass about 80 percent of full sunshine reached the soil surface. Few seedlings of any kind were ever found in

established wheat grass. Any ruderals in an invaded area were soon suppressed and died. Exceptions were *Hordeum pusillum* and weedy species of Bromus. *Festuca octoflora* and *Erigeron ramosus* are likewise annuals with periods of growth similar to those of wheat grass. Any others, as *Hedeoma hispida,* were incidental and of very minor significance. Growth habits of all these species permit them to share the late fall and early spring moisture with the wheat grass.

Experimental data have been presented in previous publications which show that the presence of wheat grass profoundly modified the water relations of the soil. During the drought years the penetration of rainfall was greatly reduced, the rate of infiltration of water was much lower than that in the same soil clothed with other prairie grasses, the soil was consistently several percent drier, and the resulting effects on other vegetation were marked. That these conditions persisted during several years of approximately normal or above normal precipitation following the drought will now be shown.

Relative Penetration of Water

Comparative effects of wheat grass and other prairie grasses upon the infiltration of rain were studied over a wide range of territory. Data from an upland prairie near Lincoln in May, 1946, illustrate the usual results. Two days after a rainfall of 1.5 inches, blocks of sod about 8 inches square were removed from areas dominated by wheat grass, big bluestem, and needle grass, respectively. Any pair of sods of any two grasses were taken not more than 2 to 4 paces apart, one in a wheat grass area and the other just outside. The 4 sides of the excavations occupied by the sods were smoothed and deepened until dry, gray soil showed clearly in contact with the moist soil above of distinctly darker color. Then the depth of penetration of the rain was measured on all four sides. The shallowest and deepest penetration only are recorded for each sampling in Table 2.

Table 2. Relative penetration of water in inches under big bluestem, needle grass, and wheat grass on May 25, 1946.

Big bluestem	Wheat grass	Needle grass	Wheat grass
10.5 to 12.5	7.0 to 9.0	8.8 to 9.5	4.5 to 5.0
11.0 to 14.0	6.0 to 9.0	8.5 to 10.0	6.5 to 8.0
10.5 to 13.7	4.0 to 4.5	8.7 to 9.6	5.3 to 6.1

The average depth of penetration of water under big bluestem was 12 inches, that under wheat grass was only 6.6. Average depth of penetration under needle grass was 9.2 inches but in the adjacent soil under wheat grass it was 5.9 inches. Obviously wheat grass was producing an effect upon the soil which permitted less penetration of rain than occurred under the other grasses.

These results are in agreement with those of Weaver & Albertson (1943). They report that in August, 1941, after 1.1 inches of rain, water penetrated 6.8 inches under native grasses but only 4.0 inches under wheat grass. These are averages of 16 measurements.

Rate of Infiltration

Rate of infiltration of water applied artificially by sprinkling was always found to be less rapid under wheat grass than under various other prairie grasses. In one experiment on July 15, 1946, on a level hilltop with silt loam soil, four square feet of surface soil, completely isolated from surrounding soil, absorbed 10 gallons of water in 31 minutes when water was sprinkled upon it so that it stood continuously on the surface. A similar area of big bluestem sod, a few paces distant, absorbed 14 gallons during the same interval. After an hour, a trench dug diagonally through the center of the wheat grass area revealed a maximum penetration of water of 20 inches but an average depth of penetration of only 16 inches. Under the bluestem, maximum penetration was 30 inches and average depth 25 inches. Big bluestem had an excellent, dead, surface mulch and the soil before watering was much more moist than under wheat grass. In the wheat grass, the 80 percent of the surface of the soil area unoccupied by the bases of this grass was bare. This lack of mulch is a very general phenomenon; local patches of black, unprotected and puddled soil are a common sight in spring in mowed prairies. Experiments have shown that where a good mulch does occur, rate of infiltration is two to three times as great. But even where there is a mulch the entry of water into the soil is often only half as rapid as under big bluestem, where the soil is wet usually nearly twice as deep. In one experiment soil under big bluestem absorbed 7.3 surface inches of water in 1.5 hours, but wheat grass slightly less than 3 inches.

Relative Amounts of Soil Moisture

Further inquiry into the comparative effects of wheat grass and other prairie grasses on the amount of soil moisture involved soil sampling. In the spring of 1946, samplings were made in three eastern Nebraska prairies by using a Brigg's geotome. Water content of soil was calculated as a percentage of the oven-dry weight of the soil. Data in Table 3 show the differences between pairs of samples as regards amount of soil moisture in alternes of wheat grass and in portions of the true prairie a few feet distant where wheat grass had not invaded. The soil appeared uniform in both sampling areas. The chief difference was that of moisture content.

In Table 3 it may be seen that soil under other prairie grasses contained a higher percentage of moisture than did soil under wheat grass. The difference ranged between 0.9 and 13.1 percent and there was a greater amount of moisture in each of the 36

TABLE 3. Excess percentage of soil moisture in prairie over that in alternes of wheat grass.

Location	Date	Sample	0-0.5 ft.	0.5-1 ft.	1-2 ft.	2-3 ft.	3-4 ft.
Lincoln	April 6	1	5.4	3.6	1.7	8.1	....
		2	2.0	2.1	0.9	8.9	....
		3	8.4	4.4	3.2	7.7	....
		4	2.2	1.1	1.9	4.5	....
Pleasant Dale	April 17	1	5.2	6.3	8.1	12.2	13.1
		2	4.7	7.0	2.4	8.7	8.9
Carleton	May 19	1	6.1	5.2	4.2	4.2	6.0
		2	9.4	6.8	3.3	5.1	4.6

samples from prairie. These results are similar to those obtained by Weaver (1942), who reported that in 1938, "There was always a higher water content, often 3 to 8 percent higher, in the bluestem prairie than in wheat grass." And for 1941 he stated, "The samples again showed consistently a higher water content in prairie."

These differences in rate of infiltration of water and the depth to which water penetrates may be readily explained. Wheat grass lacks the dense mass of foliage characteristic of bluestems and most other prairie grasses. Hence, it permits the beating rains to destroy the soft, crumb-like soil aggregates at the surface; fine soil particles become suspended in the water. These are carried into the soil with the water where they more or less completely clog the soil pores in the surface layer. This phenomenon has been described by Lowdermilk (1930) and Duley (1939). Consequently, the soil absorbs less of the precipitation, runoff is promoted, and erosion is accelerated. As a result, conditions of drought are more or less continuously maintained in wheat grass sod.

Before the drought, wheat grass was confined largely to certain clay soils and soils with claypans. It now covers many such areas and has spread widely into various soil types. Its root distribution was studied to obtain further information on this problem (Weaver & Darland 1949). Its roots are usually deeper and the species better adapted to drier soils than most other plants of true prairie. Under heavy grazing it gives way to bluegrass eastward and to blue grama and buffalo grass in drier areas westward. Replacement of wheat grass by more mesic species will probably occur very slowly and only over a long period of time. It may persist indefinitely where claypans are present.

EFFECTS ON VEGETATION

The result of competition of wheat grass with other species for water is shown not only by their wilting and dwarfing but also by their death. In other words, many kinds of plants were unable to survive in areas dominated by wheat grass and those that persisted were suppressed in their growth. Decrease in both numbers and species of forbs is to be expected in alternes of wheat grass.

SEVERITY OF COMPETITION IN DROUGHT

Wheat grass is dependent upon moisture in spring and early summer. During years of drought it often exhausted, by its early and rapid growth, all of the available supply of soil moisture before the warm-season prairie grasses and forbs had made much growth. During drought, relict forbs were almost entirely those with deeply penetrating root systems—characteristically leadplant (*Amorpha canescens*), blazing star (*Liatris punctata* Hook.), prairie rose (*Rosa pratincola*), and false prairie boneset (*Kuhnia glutinosa*). These were dwarfed immediately after the wheat grass invasion. With a gradual depletion of subsoil moisture, which was not replaced by current rainfall, they became fewer and fewer and mostly disappeared. This occurred even on low ground.

Relict little bluestem was easily replaced by wheat grass and during all of the years with severe summer drought any relict big bluestem was dwarfed and usually dried by midsummer. Despite the occasional less severe years, as 1935 and 1938, big bluestem and practically all other grasses finally died, except in areas where wheat grass had not invaded. Hence, in spring the pure stands of wheat grass presented a clean, dark green, monotonous landscape.

PERSISTENCE OF EFFECTS AFTER DROUGHT

Six years after the drought most prairie forbs had increased greatly in number and size, many exceeding predrought conditions in both of these respects. But in the wheat grass, forbs were few or often almost absent. They had only a few stems per plant, and these were much reduced in size. For example, *Amorpha canescens* and *Psoralea floribunda* were often 2 to 4 times as tall and proportionately larger in prairie than in wheat grass. A few seedlings were found in certain years but very few compared with the numbers in adjacent grassland. Moreover they were dwarfed and their success in attaining maturity seemed doubtful.

Dwarfing of the forbs which still persisted in 1946 and also the difficulty of establishment of seedlings of either perennial forbs or grasses were due to the great amounts of water absorbed and transpired by wheat grass. The production of a new crop of shoots in autumn and the growth in early spring while most other vegetation is still dormant greatly depletes the soil of its moisture. Losses by transpiration and evaporation from the surface soil from late March until May 20 have been shown experimentally to be more than twice as great (23.4 pounds per square foot of wheat grass sod) as that from similar areas of the warm-season grass, little bluestem.

EFFECTS ON FORBS AND SEEDLINGS

Studies on the kinds and numbers of forbs found in large patches of wheat grass on upland prairie were made in August, 1946. Five pairs of large circular areas each with a diameter of 30 feet were examined. These pairs of samples consisted of one area in wheat grass and one only a few feet distant

in big bluestem or bluestem intermixed with other perennial grasses. Each circle was laid off into small sectors and all species of forbs were listed. The numbers and the average height of individuals of species in both areas were ascertained. Twenty species of perennial forbs were found in the prairie plots but only 7 in those of wheat grass. Total numbers of stems were 4,029 and 403, respectively. Thus, in wheat grass there were only 35 percent as many species and 10 percent as many stems as in bluestem prairie. Average heights of representative species were: *Aster multiflorus* (5 and 11 inches), *Amorpha canescens* (6 and 12), *Psoralea floribunda* (12 and 17), *Solidago glaberrima* (5 and 12), and *Achillea occidentalis* Raf. (4 and 11 inches) in wheat grass and bluestem prairie, respectively. These differences are properly attributed to the unfavorable reactions that wheat grass exerts upon soil structure and water content of soil.

COMPETITION WITH BIG BLUESTEM

The development of big bluestem in 1938 and thereafter to form the big bluestem type on uplands has been recorded (Weaver & Albertson 1944). With the coming of a series of good years (1941-43) the thin stand of drought survivors of this species sometimes increased from 10 percent to form a cover that became 80 to 95 percent as dense as that on low ground before the drought (Fig. 7). Thus, after 1942, many prairies when viewed at a distance in late summer or autumn showed great belts and patches, reddish brown in color, on hilltops and slopes where the flower stalks of big bluestem with their forked inflorescences grew thickly. Quite in contrast to this outcome were the hundreds of places where the open stands of big bluestem, following the death of little bluestem, were early invaded by wheat grass. Then the bluestem was nearly always dwarfed, later suppressed, and ultimately exterminated in its former home, mostly on uplands, but sometimes on lowland as well (Fig. 8).

The breaking of a long period of dormancy in crowns and rhizomes of grasses was observed in some

FIG. 7. Dense stand of big bluestem on upland. It developed from a 10 percent mixture with little bluestem upon the death of this dominant in 1934. Crete, Nebraska. June 19, 1943.

FIG. 8. One of hundreds of "islands" of big bluestem entirely surrounded by a dense stand of wheat grass, on August 21, 1944, an exceptionally wet year. During ordinary years competition of the wheat grass prevents flower-stalk development and the foliage is dwarfed. Nearly all such patches have now disappeared as a result of the wheat grass invasion.

prairies after a single year of good rainfall and in nearly all, including areas of wheat grass, in 1942-43. In a prairie near Lincoln where this phenomenon was observed on a north hillside which had been invaded by wheat grass, three circular areas, each with a radius of 20 feet, were permanently marked. The number of places in which big bluestem occurred was ascertained as well as the total number of stems in each area. This was repeated on July 20, the following year, 1944. The number of places where big bluestem had grown from old plants increased 145 percent and the total number of stems (originally 243 to 1,453 per plot) increased 67 to 158 percent. Light was not a factor in retarding growth of big bluestem. Under normal stands of wheat grass with spikes it ranged from 12 to 38 percent of full sunshine. Under a good stand of big bluestem the light was decreased to 3-4 percent of full sunshine. The next year further gains were made by big bluestem; but during midsummer drought the plants sometimes wilted.

At Montrose, Kansas, where burial by dust and severe drought had enabled an almost continuous sod of wheat grass to develop, recovery of big bluestem was remarkable (Fig. 9). The long struggle between the declining big bluestem and the persistently increasing wheat grass sod from 1932 to 1941 has been recorded (Weaver 1943). One broad alterne many rods in length gradually decreased in width until in 1942 the bluestem had apparently all succumbed. But by 1944 the various stages were revealed by which big bluestem pushed up shoots through the wheat grass sod and finally by development of rhizomes recovered large areas which were once, at least above ground, pure wheat grass. These rhizomes from large persistent bunches or clumps of big bluestem spread outward to include circular areas

3 to 4 feet in diameter. The bunches and areas coalesced and surrounded the remaining patches of wheat grass. In the first stage of recovery big bluestem was thinly to thickly scattered in the wheat grass sod. A second stage showed the wheat grass intermixed with bluestem, where it could be observed without moving the foliage. But in a third stage wheat grass was found, if at all, only by close examination and as greatly attenuated individual plants. Often half of large areas had thus been reclaimed by big bluestem. The broad alterne was rapidly returning to big bluestem. The outcome in this very dynamic prairie area where the soil is filled with rhizomes of both wheat grass and big bluestem will depend upon the climatic cycles (Fig. 10). Potentially there are two possible crops, the wheat grass and big bluestem. True prairie with its mixture of mesic grasses and abundance of forbs has ceased to exist here.

Where wheat grass and big bluestem invaded simultaneously, much of the area has gone over entirely to big bluestem. Conversely, where big bluestem recovered in an area dominated by wheat grass it often appeared in spring that the bluestem might be gaining ground. But later it was nearly always retarded in its development, if indeed it did not dry as a result of drought, which was always most severe in wheat grass. Sometimes local showers greatly aided the bluestem. Thus, with remarkable exceptions already noted, any progress in its replacement of wheat grass over a general upland area has been slight.

Where wheat grass invaded lowlands as in bottoms of ravines and temporarily replaced the taller grasses, such as big bluestem and tall panic grass and sometimes also slough grass, usually the dormant tall grasses have reclaimed the area. This has been observed in many places, including level bottomlands. But the recovery does not indicate that the rhizomes of wheat grass have died or decayed. With drought, wheat grass vegetation may once more appear. It sometimes remains in pure stands on the steep upper banks along ravines where much precipitation is lost by runoff.

FIG. 9. Development of big bluestem from dormant crowns in wheat grass sod. Montrose, Kansas, 1944.

NEEDLE GRASS CONSOCIATION

The remarkable manner in which needle grass spread during drought into semibared areas regardless of slope and even onto low ground formerly covered by big bluestem has been reported (Weaver & Albertson 1944). This spread was so great that this type was surpassed in area only by those of wheat grass and mixed prairie (Table 1). The stands of needle grass, which were often 80 to 90 percent pure, had thickened and the plants matured until they had the appearance of climax vegetation (Fig. 11). Since 1943 there has been little or no extension of the communities of needle grass. Neither have the Stipa-covered areas decreased perceptibly as a result of invasion. The chief changes have been a further thickening of the stands both by an in-

FIG. 10. Return of big bluestem from dormant crowns (dark belt) in a portion of the prairie at Montrose, Kansas, which had been completely invaded by wheat grass in 1941 after several years of drought. June 17, 1947.

FIG. 11. A south-facing hillside at Crete, Nebraska, almost denuded of little bluestem and then invaded from the hillcrest by needle grass which, on June 19, 1944, formed almost a pure stand 18 inches tall but did not flower.

crease in the basal area of the established bunches and by an enormous increase in the number of seedlings and small clumps of all ages. Sometimes the bunches are so small and numerous as to present a tufted sod rather than a bunchy appearance. Extremely large seed crops have been produced and 10 to 20 seedlings per square foot have often been found.

When mowed annually, needle grass alone does not form a good soil mulch. In certain years much bare soil is visible in early spring. Often the cover formed by weedy bromes is absent because of drought, but where *Bromus commutatus* is present, it forms an efficient soil cover. Elsewhere, June grass, sideoats grama and even bluegrass occur. Most deeply rooted perennial forbs had succumbed to the drought and they now occur only sparingly because of the crowded population of needle grass which, like wheat grass, grows vigorously in late fall and renews growth early in spring. Indeed, a natural thinning of the grass population as the older and better established plants rob their offspring of water must occur in forming the usual widely spaced bunches characteristic of predrought stands. The present communities are also unlike those of predrought times in the absence or small numbers of intermixed prairie grasses, the lack of an understory, and the absence of a continuous even if a thin mulch.

PRAIRIE DROPSEED CONSOCIATION

Prairie dropseed spread down the slopes from the drier upland sites which it shared with needle grass often to the edge of ravines. The myriads of seedlings established during the least severe years of the drought rapidly grew into tufts and then into large bunches. Once a good stand was attained, other grasses and forbs had difficulty in becoming established.

This spreading into new territory continued in some prairies until 1946. Thus, prairie dropseed even in some extensive prairies easily became the most abundant species. Where it grew in pure stands, the lodged leaves usually formed a more or less complete ground cover. They remain attached to the stems. The three-foot flower stalks occurred thickly and over wide areas. In the normal development of the crown the bunch is elevated an inch or more above the soil surface. Erosion had often occurred about long-established but widely spaced plants so that the crowns were three inches above the soil. In many drought-born alternes with sharp ecotones into old, long established prairie, the radial span of the foliage flattened by winter's ice and snow was over two feet. In many places the new stand was invaded even in the bunches following the general recovery by big bluestem. This tall grass overtopped the dropseed and hindered its growth by shading. The roots of big bluestem also penetrated more deeply for water. Thus, some areas of prairie dropseed may be replaced by big bluestem.

INDICATORS OF DELAY IN RECOVERY

As one surveyed the prairie three to five years after the drought, marked changes in the community relationships were apparent. But certain other phenomena resulting from the years of drought were also impressive. Among these were the persistence in places of certain species in the marked overabundance they had attained when the soil was bared. Another feature was the presence of certain invading species which had apparently become rather permanent constituents of the prairie. But most pronounced of all was the great upsurge of vegetative development of practically all prairie plants during and following the wet year, 1944.

During drought certain native forbs profited by the death of their competitors and increased very greatly (Weaver & Albertson 1939). Chief among these were *Aster multiflorus, Erigeron ramosus, Solidago glaberrima* and *Specularia pefoliata.* A remarkable increase of other species, formerly of little importance, but with some type of underground storage, occurred. These included *Ionoxalis violacea, Allium mutabile, Anemone caroliniana, Tradescantia bracteata,* and later *Gentiana puberula. Hedeoma hispida* and *Plantago purshii* also became very abundant. The last two annuals disappeared early with the introduced weeds. But in many places, the thick though dwarfed stands of Aster or Solidago, the snow-white masses of Erigeron, Gentiana scattered abundantly, and, most persistent of all, the great abundance of Ionoxalis in the understory, continuously reminded one that these were remnants of the drought flora which had now been reduced to their usual predrought abundance except in those places where the grass dominants were still few and widely spaced.

In various wheat grass prairies certain subsere species common during drought still prevailed locally in the understory. Among these were *Plantago purshii, Specularia perfoliata, Ionoxalis violacea* (often in very great abundance), *Hedeoma hispida,* and *Lepidium densiflorum.*

Sand dropseed, a dominant of mixed prairie, had invaded drought-bared pastures in the true prairie region in a remarkable manner in 1935 to 1940 (Weaver & Hansen 1941). It also became common but not generally distributed in several of the prairies. It invaded only where the soil was bare. Although rapidly waning by 1946 where the cover became dense, it still persisted in late subsere stages and sometimes it was quite abundant in wheat grass and perhaps less so in blue grama. In a series of quadrats in thinned native pasture, the number of stems per square meter decreased only from 6,127 to 2,882 or 53 percent by 1943. But with the rapid return of the bluestems their number again decreased by 53 percent by 1946. Dense shade and thick mulch, whether produced by bluestems or bluegrass, reduced the number of stems of sand dropseed, the degree of tillering, and amount of seed production. Re-establishment by seedlings was difficult and upon the early

death of the old plants the species locally disappeared. But in certain wheat grass prairies, especially, sand dropseed still prevails.

Side-oats grama will long be remembered as one of the grasses which played a spectacular role during certain years of drought. In a few prairies, belts of this grass in almost pure stands covered the steep shoulders of wind-swept slopes as late as 1945. Isolated large bunches were common. These belts and very large bunches exhibited in a small way the development of this species over vast areas of prairie during certain years of the great drought. Its persistence in abundance is a constant reminder of the lack of stabilization. In predrought prairies it nearly always occurred as small, isolated, rather open tufts, scattered among other species (Weaver & Fitzpatrick 1932).

The lingering presence of hairy chess in many prairies is distinctly a postdrought phenomenon. Dense patches of *Panicum scribnerianum* developed during drought still occur, especially in places where drought damage was severe. Conversely, *Carex pennsylvanica* of widespread abundance during drought, although still found in unusual amounts, is gradually being suppressed to its former place in the understory. But many species of sedges have become far more abundant than formerly both on upland and lowland.

Eragrostis spectabilis, formerly an interstitial species of infrequent occurrence, became extremely abundant in the years immediately following drought. It still persists in numerous patches in both prairie and pasture and is many times more abundant than formerly. It is manifesting considerable stability.

Muhlenbergia cuspidata, a drought resistant species of mixed prairie, entered most of the disturbed prairies and spread to new locations year by year. It now occurs in small patches in most prairie tracts and even as well developed alternes on many eroding upper slopes. It seems to compete well with the bluestems and other prairie dominants and tenaciously retains its stand.

Certain new forbs have been added to the flora, at least in the sense that species heretofore sparse or rarely seen have become common to abundant. *Geoprumnon plattense* is an example of a legume that had spread over much of the drought area.

ROLE OF BIG BLUESTEM

After the long drought the dormant sods of big bluestem resumed growth as single or few-stalked plants. This grass began recovery in 1941 (Fig. 12). Among all the grasses that flourished so remarkably in 1944, the growth of this species was most impressive. That year witnessed the best development of vegetation in a decade. Moreover, by this time the driest slopes were well covered with grasses. By mid-August plants of the uplands and even on the hilltops had produced a great abundance of flower stalks 5 to 5.5 feet high. These were tipped with the forked inflorescences. Patches and strips of openly spaced bunches spread for many rods over the ridges and upper slopes. Others, extended down the slopes and merged with the areas of big bluestem at their bases. The stand almost everywhere was open because of rapid, widespread propagation by rhizomes. In the few places where it was pure and dense, flower stalks were shorter. Because of its greater stature, its deep shade overshadowed most other grasses. When fully developed in August, the foliage was 2 to 2.5 feet high on the uplands.

FIG. 12. Relict big bluestem that has developed from long-dormant rhizomes. Crete, Nebraska, July, 1943.

A similar upsurge did not occur in undisturbed patches of bluestem prairie. Here the grasses, despite the increased rainfall, were not so rank. They had far fewer flower stalks and these were conspicuously more slender and shorter even in comparable or better sites. The irregularity in height of the new cover in drought-bared areas compared with that in undisturbed sod-bound patches which escaped such destruction was very conspicuous. In the following years big bluestem gradually thickened, often to nearly pure stands, and occupied much territory in which, before the drought, it had composed only a small percentage of the vegetation.

Where big bluestem grew between the bunches of prairie dropseed or had come up in them, it was clear that the dropseed was growing less vigorously. By 1946 big bluestem had spread over many uplands to form open but continuous patches in and between the bunches of this species. It flourished almost as if no other grasses were present. It occupied the bare space resulting from drought. The drought-swept hilltops now often apeared like a lowland meadow, half of the vegetation being big bluestem. The irregular appearance caused by the bunches of prairie dropseed had disappeared since big bluestem filled the interspaces and spread its rhizomes through the bases of the bunches. Its great height-growth, its deeper roots, and its sod-forming habit placed the bunch-forming prairie dropseed at a disadvantage during wet years. In many places, big bluestem seriously threatens the dominance of this grass (Fig. 13).

FIG. 13. A sod of big bluestem growing around and up through a bunch of prairie dropseed. The general foliage level of the dropseed is about 16 inches; height of the bluestem is nearly twice as great. Photo near Lincoln, August 20, 1944.

In some prairies big bluestem in 1944 was invading the sod of blue grama established during the drought (Fig. 14). Some patches had been obliterated by the thickening of the invaders to form a nearly complete overstory. General invasions where the bluestem-blue grama ecotones had formerly been very narrow were studied in detail. At first the bare soil which normally surrounded patches of blue grama was occupied, then the rhizomes advanced under the sod a few inches each year. Relatively new rhizomes only 2 to 3 years of age were found arising from much older ones. They extended 3 to 4 feet into the territory of blue grama. Conversely, inward from the newly established front of the invading bluestem, the short grass became thinner and more attenuated foot by foot as the tall competitors became thicker. The number of shoots gradually decreased until finally only the decaying dead plants remained. This was observed in many places and along invading fronts several rods in length. Under annual autumnal mowing, it seemed to require three years for big bluestem to exterminate the once-abundant blue grama or buffalo grass.

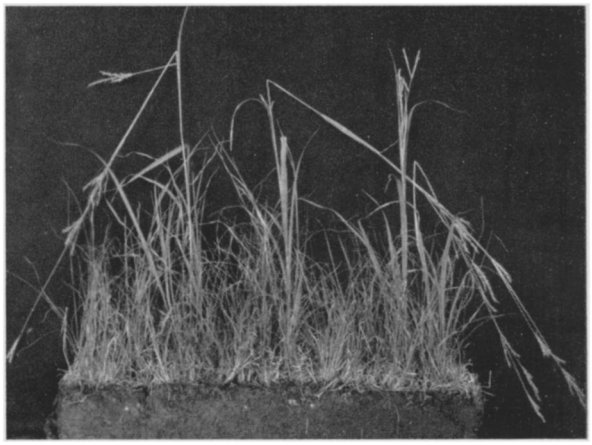

FIG. 14. Early development of a sod of big bluestem which is growing in a cover of blue grama, formed during the years of drought. Valparaiso, Nebraska, Sept. 1944.

Many outposts of short grasses were much invaded in 1944. However, the short grass was completely ousted even locally only after two or three years of dense shading. It should be emphasized that by 1947 total foliage almost everywhere was a fourth to even a third denser than during seasons with normal precipitation. The sod had thickened by an unusual development of most species. Hence shade was very dense. In one prairie near Hebron, Nebraska, where north-facing slopes had been more or less clothed with blue grama during drought, big bluestem now occupied 75 to 98 percent of the land and blue grama was found only in small but numerous islands, which were much shaded by its tall competitor.

The spreading of big bluestem in the years following 1944 was marked in almost all the prairies studied except where wheat grass thrived. Most advanced were single shoots, then small to large bunches, and lastly the closed ranks of this tall grass. The large amount of litter in one prairie where the grasses were left unmowed was perhaps as much of a detriment to the shorter grasses as the shade produced by the current new growth.

LITTLE BLUESTEM AND THE RETURN OF ITS TYPE

Little bluestem was the first major species to decrease greatly in drought; it also suffered the greatest losses, and it was the last to reappear. At the end of the drought it was of only intermediate importance and was outranked by six other dominant species. Of 12 sample prairies examined, scarcely a trace of little bluestem remained in half of them, in others it was rare, and only in portions of two was it abundant (Weaver & Albertson 1943). Since this species began to recover very tardily and mostly not until 1941, the space it vacated was appropriated mainly by the rapid spreading of big bluestem, which was previously associated with little bluestem, at least in small to moderate amounts.

When good rains fell, crowns of little bluestem which had previously supported only a few stems became two-thirds filled with them. Flower stalks developed, seeds were ripened, and seedlings and small tufts of little bluestem were common in 1943. The major return, however, was by the awakening of crowns that had put forth few or no green parts above ground but remained dormant for 5 to 7 years. During 1944 the plants, from whatever source, flourished. In former stands of little bluestem where there was survival, the stems were often 2 to 2.5 feet tall. This grass occurred often as widely scattered bunches and increased greatly in or near places where its survival was greatest. Small tufts rapidly expanded into large ones and where drought had not entirely destroyed the plants the return was fairly rapid, but only moderate compared with big bluestem. The bunches became extremely well filled with stems, seedlings produced many new bunches, and by 1946 it had spread considerably and also thickened its stand. Once again certain uplands took on the appearance of climax prairie with little bluestem as the chief dominant. Considerable little bluestem reappeared in upland stands of big bluestem. Mixture of two-thirds little bluestem and a third big bluestem with a few other grasses became common; parts of prairies with a dominance of 90 percent little bluestem can now be found. Despite these exceptions, it will probably require a long period of adjustment for little bluestem to resume its general dominance over big bluestem wherever the latter occurs in great density.

Where blue grama had invaded its territory, the old crowns of little bluestem sent forth new shoots without regard to the presence of the invader, a phenomenon that has been noted for nearly all species of dominant prairie grasses as well as forbs (Fig. 15). With the return of little bluestem a cover of litter was rapidly formed.

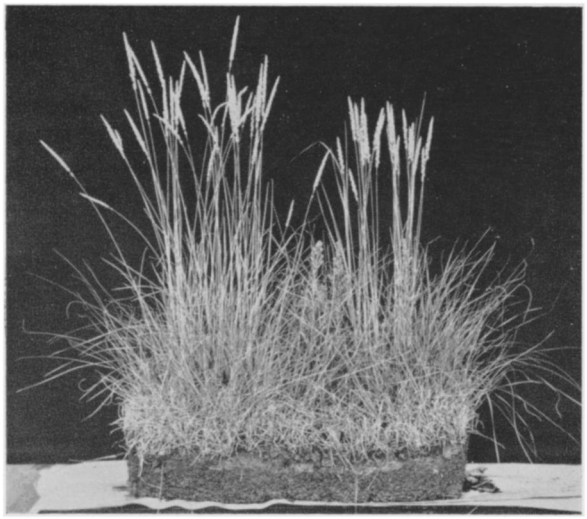

FIG. 15. June grass (*Koeleria cristata*) growing in a dense sod of blue grama, illustrating the replacement of this drought invader by various species of grasses and forbs which grew up through the short-grass sod.

Conversely, in some former little bluestem prairies little bluestem is now rare or absent. In a few places it has revived in local areas taken over by wheat grass during drought. These it seems to be reclaiming. Final study in 1948 showed the dominance of little bluestem and the suppression of wheat grass. A few local areas where prairie dropseed became very abundant and approached a pure stand during the later years of drought are now largely repossessed by little bluestem. Its return in abundance in many drought-populated places and in relict areas was spectacular.

A comparison of the appearance of the relict little bluestem type in its remaining alternes with that of adjoining areas was made in 1946. An undisturbed area in mid-May was evenly populated with numerous grasses with an average height of 8 inches. The grasses formed a continuous carpet which had a very uniform appearance. There were no weeds and no hairy chess occupying interspaces. The cover of debris was moderately thick and continuous despite annual mowing. No bare soil was exposed. Little bluestem was of the tufted sod-mat type and did not occur in large bunches. The soil surface was smooth and not visibly eroded even on steep upper slopes. Numerous prairie forbs were evenly distributed throughout and did not occur in local, dense, controlling stands. Side-oats grama, penn sedge (*Carex pennsylvanica*), and June grass were at a minimum. A small amount of bluegrass, *Antennaria campestris*, *Viola pedatifida*, Scribner's panic grass, and rosettes of Senecio grew in the understory. Seedlings of grasses and forbs were rare since the vegetation was of the closed type. The balance between climate, soil, and vegetation had been attained; it was climax prairie.

But in adjacent, drought-damaged areas the lack of stabilization was revealed in many ways. One or two, or at most three species of grasses dominated. Often these included side-oats grama, June grass, or other species of relatively small importance in the climax. The vegetation was very irregular in height varying with the density of stand. Many plants were suppressed, others were twice their stature in stabilized prairie. June grass, for example, had attained heights of 16 to 21 inches; the spikes were long and dense. In prairie, where competition was severe, the height was only about 14 inches and spikes were proportionately smaller. The cover of vegetation was incomplete. Much soil was exposed. In places the first inch of soil had been removed by wind and water, the surface was irregular. There was not a continuous, stable, protecting mulch. Kinds of forbs were few, some grew in unusual density. There was no understory except of scattered patches of seedling grasses and forbs.

SPREADING OF KENTUCKY BLUEGRASS

Bluegrass was absent at the end of the drought from all but a few of the most easterly prairies. Before the drought it nearly always formed 5 percent or more of the vegetation (Weaver & Fitzpatrick

1934). But where little bluestem died of drought, bluegrass also succumbed. It remained only where relict little bluestem and big bluestem continuously furnished shade. But in 1941 bluegrass recovered in patches in ravines and spread across the upper flat portions of these onto the hillsides where run-in water or melting snow furnished an additional supply of moisture. A good crop of seed was produced. Thereafter it spread across ravines and up adjacent slopes, completely covering much open soil and forming a thin understory to whatever prairie grasses were in possession, except wheat grass or blue grama.

By 1944 it had taken over and consolidated its holdings in much semibared soil. Like other cool-season grasses it made great use of the water supply in early spring, and like all prairie species at this time seemed greatly rejuvenated by the decreased competition. Its continuous dominance over local areas denoted severe previous disturbance. Where seral species as sand dropseed and many-flowered aster occurred, they were gradually reduced in size and numbers by the bluegrass sod. Since its invasion into many bare areas occurred immediately after drought and its network of dense rhizomes and efficient masses of roots filled the soil, bluegrass now has possession of numerous large patches of prairie. Some of these occur on low ground, mostly in or on the banks of ravines, but not a few on ridges and other dry sites. In fact, in 1944 it became common almost everywhere as an understory, except in certain drier, western areas. Eastward it invaded areas of short grass and to a lesser extent those of wheat grass, especially the more open stands. Wherever bare interspaces occurred bluegrass rapidly threaded them with rhizomes. It was an important species in restoring the soil mulch which was almost absent during drought. This was especially conspicuous in certain communities of needle grass where the mulch, next to wheat grass, was the last to develop. In general, bluegrass became very widely distributed. It occurred in small amounts in the more moist places of even the driest prairie, and thrived under big bluestem and other warm-season grasses. An exception in many places was its small amount or absence in alternes of nearly pure prairie dropseed. Usually only small amounts, if any, were found intermingled with the cool-season grasses as western wheat grass and needle grass, since here even in spring soil moisture was less plentiful. Where invasion had occurred, this was sometimes indicated by the sparse stand, dwarfed flower stalks, and small inflorescences.

Bluegrass has now reached its predrought cover of 4 to 10 percent of the vegetation in many prairies. In some this amount is greatly exceeded where it almost alone has replaced the early postdrought understory of *Bromus tectorum, B. commutatus,* and certain other annual grasses. Even in the most westerly true prairies it is gradually becoming widespread. The large size and vigor of the plants (sometimes flower stalks 3 feet tall stood thickly on upland), their enormous seed crops, and the rapid spread over hilltops and dry slopes were one of the striking features of revegetation.

ESTABLISHMENT OF SEEDLINGS

Bountiful crops of seedlings were produced following the years of desiccation of the soil. Conditions for growth of seedlings in both 1942 and 1943 were excellent. In 1942, for example, the surface of the soil under the rapidly developing grasses was damp practically all spring and mostly throughout June, not only because of rain and heavy dew but also because of much cloudy weather. Moreover, the vegetation itself was becoming denser and furnished considerable protection to the seedlings from direct isolation, a condition which is favorable to their early development.

"In 1943 one was impressed by a new phenomenon, that of different stages of development of the several species from seedlings to small bunches. By midsummer, seedlings of the previous year were rooted 1.5 to more than 2 feet deep, and still older bunches more deeply. The oldest were beginning to produce flower stalks and thus indicated both successful ecesis and a permanency of the cover" (Weaver & Albertson 1944).

By 1944 remaining interspaces in the prairies were being populated by seedlings of various grasses, by offshoots from established plants, or by the late recovery of grasses from dormancy. Seedlings of needle grass, June grass, bluegrass and side-oats grama were often most abundant and most widely distributed but those of tall dropseed, prairie dropseed, blue grama, and big bluestem were often plentiful. One- and two-year-old plants of many grasses were common. Still older ones showed their youth by producing only one or a very few flower stalks.

Little replacement of the forb population occurred over a period of 6 to 7 years, since failure to complete vegetative growth or to blossom or ripen seed was usual. Seedlings of forbs were rare in 1941-42, but many forbs which had vanished from all but relict patches of little and big bluestem prairie returned after a year or two of good precipitation. By 1944 seedlings of some forbs were plentiful in places but they were far more abundant, more varied, and of more general occurrence in following years. The process of reseeding interspaces among the thickening vegetation and small bare places wherever they occurred continued in 1945 and 1946.

NEW SOIL MULCH AND RETURN OF UNDERSTORY

A good soil mulch consisting of plant debris so completely covered the ground in many prairies by 1944 that almost no soil was left bare. This was true not only in the relict prairie types but in much other vegetation as well. In fact the greater density of vegetation, the establishment of a good mulch, and the beginning of the return of the understory were prominent features of the vegetation in 1944. Where best developed this layer of debris was one-half to

three-fourths inch thick and often continuous, a phenomenon not seen since 1934. The presence of the mulch all over areas where the black bare soil had been exposed for nearly a decade was very impressive and denoted great change in environment. The driest places in the prairie, including the breaks at the tops of steep banks, now had a good cover of debris. This was often furnished by June grass, side-oats grama, and bluegrass.

Every species of plant contributed something to this layer of debris, but certain species much more than others. June grass, prairie dropseed, bluegrass, blue grama, side-oats grama, and hairy chess were all among the more efficient.

June grass, commonly an interstitial species, formed a continuous sod over many rather large open spaces. It was often abundant in the needle grass type, but not generally so. While the young tufts were sometimes only 1 to 2.5 inches in diameter, the top spread was 6 to 8 inches. Thus, although the plants were 2 to 4 inches distant, they formed a good stand with nearly all of the soil covered between the bunches. They often occurred abundantly in wheat grass sod where 2 to 3 bunches per square foot were not uncommon. The mulching effect of the dead but attached leaves was pronounced. They extended 4 to 5 inches outward from the base of the tufts and in spring often completely concealed the new shoots of little bluestem beneath them. The dark-green colored patches of this species appeared over the landscape like the shadows of small clouds.

June grass is relatively short lived. It is not a good competitor and it has been gradually relegated by needle grass, bluestems, and other more stable grasses to its former place as an interstitial plant. But during this process it added considerable mulch to the soil.

The narrow, greenish-yellow leaves of prairie dropseed, which curve outward and downward in summer, lodge thickly in winter in such a manner as to provide a mulch to a distance of 10 to 14 inches around the base of the plant. Old patches present a complete dense cover of lodged leaves. It may be partly due to this dense debris that few forbs or other grasses occur here. Often there is no bare ground (Fig. 16).

FIG 16. Bunches of prairie dropseed in early spring, showing the thick mass of widely spreading and lodged leaves still attached to the crown. The new growth is erect. May 20, 1947.

An excellent type of soil mulch was furnished by bluegrass. It was often the greatest contributor both to covering the open soil and to producing a thick mulch. Where the stand was thick no soil was visible and the dead mulch was 2 to 3 inches deep. Such a mulch may be distinctly harmful to other grasses, especially in the seedling stage. Side-oats grama also furnished much debris, although the bleached dead leaves for a time remained attached to the stems.

Hairy chess has gradually disappeared from many prairies and its abundance is greatly reduced in all. It has been replaced by more stable, perennial grasses. But its role in preparing and maintaining a mulch should be emphasized. Thick local stands in small bared places often had 20 to 25 stems per square inch and a height of 10 to 12 inches. Even after it disappeared in areas of true prairie in 1945-47, it still persisted in patches of short grass. The plants not only grew thickly in the openings in the mats and in the bare spaces surrounding them, but the whole sod mat itself was overtopped by the panicles of hairy chess. This maintained although the blue grama foliage was 8 inches high and the flower stalks 15 inches or more. This dense growth was often a detriment to the short grass for not only did it decrease the water supply but also greatly shaded and often almost obscured the 8- to 9-inch foliage of blue grama. In places the dead debris in blue grama was 2.5 inches thick.

Hairy chess persisted as long as bare spots were available between the bunches of needle grass or prairie dropseed. Where the bunches were open this weed grew within them. Even when local drought occurred, the stands were thick although the stems were dwarfed.

In stands of wheat grass, hairy chess may still persist. For many years it formed a more or less complete understory and often produced considerable mulch as has already been described.

Exceptions to the more or less general presence of a well developed mulch occurred as late as 1946-47. In pure stands of needle grass the mulch was sometimes only partial. Under newly established prairie dropseed, where the plants were not densely aggregated, bare black soil still occurs. In the mixed grass type of somewhat open stand 20 to 30 percent of the bare soil was free from any cover of dead vegetable matter.

RETURN OF FORBS AND RE-ESTABLISHMENT OF SOCIETIES

By 1944 the forbs had nearly all increased greatly in stature. This was one of the most outstanding features of the prairies but it was nearly confined to those of the relict bluestem type. Here too they first increased in abundance. Excellent examples are *Amorpha canescens, Psoralea floribunda, P. argophylla,* and *Helianthus rigidus* (Cass.) Desf. These were nearly all old, well established plants. The increase was mostly in height-growth, abundance of foliage, and number of stems. In some prairies a predrought stand was almost attained by *Psoralea*

floribunda; Helianthus rigidus produced large plants without much increase in numbers. Dwarfed, single-stemmed plants of *Baptisia leucophaea* Nutt. now developed 4 to 5 stems of normal size. The very deeply rooted *Kuhnia glutinosa* often produced 20 to 40 vigorous stems where only a few dwarfed ones grew before.

By 1944 *Rosa pratincola* was very abundant in local but extensive patches. When in blossom the plants were readily located from a distance by the delicate fragrance of the flowers. In dense societies 20 to 40 blossoms occurred per square meter. The red buds and white, pink, or rose-colored flowers were found mostly at the upper foliage level of the grasses in June. So deeply are the plants rooted and so little shade is produced that often they did not noticeably affect the abundance of the grasses.

Increase in stature was not apparent in some prairies even in 1944. Societies of forbs were few, highly localized, and almost confined to ravines and other favored sites. The following were becoming more plentiful where their stand had been greatly depleted: *Meriolix serrulata, Aster sericeus, Sisyrinchium campestre, Liatris punctata, Solidago glaberrima, Artemisia gnaphalodes, Silphium integrifolium* (locally), and westward, *Solidago mollis.* But many of these were not yet present in normal abundance. About 20 other species were again seen occasionally, some for the first time since the drought. Among these were *Petalostemum candidum, P. purpureum, Vicia americana, Delphinium virescens, Salvia pitcheri,* and *Hieracium longipilum.* Despite these gains the general aspect in the prairie everywhere was that of grass with only occasional forbs; a longer time was necessary for the re-establishment of the societies.

In 1945 forbs were much less localized than before; greatly disturbed areas were being populated as well as relict types. It was now also clear that some had spread widely and occurred in sites where they were not found before the prairie grasses had been greatly depleted. *Psoralea argophylla* had not only far exceeded its predrought abundance in many prairies but spread over the driest hilltops as well. *Ceanothus pubescens* (T. and G.) Rydb., formerly quite local on upper slopes, had now spread widely and the stand had thickened greatly. *Geoprumnon crassicarpum* showed an enormous increase in both numbers and distribution. Its societies were far more extensive than under normal stabilization of prairie. Plants of *Baptisia leucophaea,* normally rather widely spaced and largely confined to lower slopes, now grew on the uplands as well. Some societies were so dense that the tops of the plants were in contact with each other over several square yards. *Vicia americana,* commonly found on low ground, now occasionally flourished on the hilltops.

A remarkable increase in numbers of many species had been attained. Stems of *Helianthus rigidus* had increased greatly; there were sometimes 30 to 60 per square meter. *Amorpha canescens* was greatly overdeveloped, often 9 to 15 very tall and very leafy stems were counted per square meter. Plants of *Liatris punctata* were often 5 to 10 times more abundant than before the disturbance caused by drought. *Psoralea floribunda* grew so thickly in some prairies (outside the wheat grass and needle grass types) that in early summer the whole area appeared as a single society of this legume. Plants of *P. esculenta* were especially large, thrifty, and overabundant. *P. argophylla* had increased to 100-130 stems per square meter in 1947. Certain prairies westward where forbs had been few, now displayed a considerable variety. Twelve distinct societies were recorded in 1945. In most prairies, other than needle grass and wheat grass, societies of many of the species mentioned occurred for the first time since the great drought. Societies of at least 25 species were repeatedly observed.

In addition many other forbs were returning in greater or less abundance, some as *Echinacea pallida, Pentstemon cobaea, Hosackia americana, Polygala alba, Anemone cylindrica,* and *Fragaria virginiana* were seen for the first time since drought. Among these later arrivals were *Comandra umbellata, Agoseris cuspidata, Viola pedatifida, Mesadenia tuberosa, Glycyrrhiza lepidota,* and *Heliopsis scabra.* Others had persisted only in ravines.

The heavy rainfall following the years of drought had now wet the soil for many feet in depth and all plants including the most deeply rooted had benefited greatly. All were of unusually large size and many grew more thickly than the writer had ever seen before. This was especially true of *Amorpha canescens; Psoralea floribunda* often had 100 to 120 stems per square meter on the hills and twice as many on lower slopes. While the usual number of flower heads of *Helianthus rigidus* when growing in prairie is only 1 to 3, they now varied from 3 to 7 and all were much larger than normal. *Rosa pratincola* had greatly increased and in many places in relict bluestem prairie formed one-third to one-half of the entire plant cover. Since this species often has roots 18 to 20 feet in depth, propagates by underground parts, and attains a considerable height even when mowed annually, it may be many years before it is reduced to its usual predrought status. In one large prairie *Ceanothus pubescens* had migrated from the upper slopes downward to banks of ravines. Small plants were scattered over the entire hillside. That they were young and had had little time for reaction upon the new habitat was shown by the presence of prairie grasses beneath them. These are regularly ousted by the shade of well developed clumps or, at best. only bluegrass remains.

The large size and enormous crop of fruit produced by *Geoprumnon crassicarpum* was remarkable. Seventy five to 95 unusually large fleshy pods were counted on single plants. *Sisyrinchium campestre* was even more abundant than reported in 1944 (Weaver & Albertson), since many of the few-stemmed plants had now developed into large clumps. *Hieracium longipilum* previously found as isolated individuals was not infrequently well aggregated, 10 to

20 rosettes occurring in a single square meter. In patches on lower slopes plants of *Liatris scariosa* occurred at the high rate of 10 per square meter.

Among plants late in appearing after the drought were *Lithospermum gmelini* (Michx.) Hitchc., *Lespedeza capitata, Meibomia illinoiensis* (except in ravines), *Glycyrrhiza lepidota, Petalostemum candidum,* and *Viola pedatifida.* Although there was a steady increase in number and size of societies of forbs, only in relict prairie did their distribution approach a predrought norm. Where the cover had been greatly depleted certain species grew in unusual abundance but in some prairies only, while many forbs formerly present were not found.

When one compared the forbs in even a small piece of upland prairie which had been little disturbed by drought with an adjacent area of similar size which had been drought-swept, marked differences were found. For example, in 1946 the flora in and adjacent to an old prairie road running down a steep west slope was compared with that two rods beyond. Of 24 species of forbs found in the slightly disturbed prairie, 12 were not found in the adjacent area. In a similar comparison of a drought-swept place on the hilltop and another adjacent site on an upper north slope, 16 species were found in the more protected area only. Nine of 11 others also grew in the drought-disturbed area, but in much reduced numbers.

The understory vegetation is returning only slowly and even seven years after the drought the ground layer is far from complete. Thus, despite great increases in numbers of forbs, and even an overabundance of certain species, the total population is still far below that preceding the catastrophe of drought. Moreover, distribution is not so uniform. Thus, the effects of drought are still plainly to be seen by any one who can interpret the prairie landscape.

SUMMARY

During the three years (1941-1943) following the seven years of devastating drought, the true prairie of the midwest had succeeded in repopulating most of the bared soil. But a series of changes in the vegetation seemed inevitable before predrought stability could be attained.

These changes included an increase in the former dominants, suppression of drought dominants under the wetter phase of the climatic cycle, disappearance or suppression to normal numbers of other relict drought populations, and an increase of drought-depleted forbs. Other necessary changes were a new development of societies, reduction in height-growth with the return of increased competition, re-establishment of the understory, and the building of a soil mulch. These phenomena have been studied during a period of five years very favorable for stabilization.

Extensive predrought surveys (1928 to 1933) revealed the presence of only three major upland communities of prairie. The dominant of the needle grass (*Stipa spartea*) consociation was greatly thinned at the inception of drought. But later, in addition to holding its own territory, it spread widely and after 1943 formed the third most extensive community. Prairie dropseed (*Sporobolus heterolepis*) ranked as only a small consociation preceding drought. It not only recovered its losses during drought but also increased its territory enormously. But it still ranks lowest in extent among the eight present-day prairie types.

Little bluestem (*Andropogon scoparius*) was formerly the most abundant of all prairie grasses. It formed the third and by far the most extensive consociation of upland true prairie. But losses were so severe and readjustments so great that by 1943 the largest portion of it was occupied by a relict big bluestem (*A. furcatus*)—little bluestem type, and the remainder by a big bluestem type and one of mixed grasses.

In addition to these five old or modified types, three new ones (western wheat grass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), and mixed prairie) had developed. The area occupied by mixed prairie is largest, western wheat grass second, and needle grass third in the greatly disturbed true prairie west of the Missouri River.

The persistence of communities of wheat grass and their marked effect in modifying the water relations of the soil are most impressive phenomena. Wheat grass has not extended its area since the bared soil was reclaimed by other perennial dominants. Only rarely has it surrendered its control over very extensive areas occupied during drought.

Wheat grass, unlike other prairie grasses, develops a very inefficient mulch. Often the soil remains nearly bare. Hairy chess (*Bromus commutatus*), a chief species of the understory, often forms a good mulch. An understory of blue grama may also occur. A few prairie grasses invade wheat grass areas in wet years, but competition for water is too severe to permit general invasion.

The presence of wheat grass retards rainfall penetration or infiltration of water applied artificially, often to the extent of 35 to 50 percent. Extensive sampling has shown that the soil is always much drier under a wheat grass sod than under adjacent prairie grasses. The bare soil or meager mulch permits beating rains to destroy the soft crumb-like soil aggregates at the surface; fine particles are carried into the soil with the water and more or less completely clog the pores in the surface layer.

Competition of wheat grass was so severe in drought that other grasses and even very deeply rooted forbs were dwarfed or died. Dwarfing of forbs still persists. The difficulty of establishment of seedlings is due to the large amounts of water absorbed and transpired by this early, deeply rooted, sod-forming species which is active also early in spring and late in autumn.

Where very open stands of big bluestem alone remained on upland when little bluestem died, invasion by wheat grass usually resulted in suppression

of the bluestem. But where big bluestem was more abundant and firmly intrenched but dormant, invasion by wheat grass was sometimes unsuccessful. Any progress in the replacement of wheat grass in upland areas has been slight.

The present needle grass type is unlike that of the predrought community in the absence or small numbers of intermixed prairie grasses, a paucity of forbs, the absence of an understory, and the lack of a continuous mulch.

An indicator of delay in recovery was the persistence in places of certain species in the marked overabundance they had attained when the soil was otherwise bare. Chief among these were *Aster multiflorus, Erigeron ramosus,* and *Solidago glaberrima. Ionoxalis violacea* and *Anemone caroliniana* are examples of similar species with organs for underground storage of food. Examples among the grasses were side-oats grama (*Bouteloua curtipendula*) and purple lovegrass (*Eragrostis spectabilis*), and the lingering presence of sand dropseed (*Sporobolus cryptandrus*) and hairy chess.

Another indicator of incomplete recovery was the presence of certain invading species which had apparently become rather permanent constituents of true prairie. Examples are *Muhlenbergia cuspidata* and *Geoprumnon plattense.*

The great upsurge of vegetative development of practically all prairie plants during and following the very wet year, 1944, was pronounced.

Spreading of big bluestem following 1944 was marked in portions of all of the prairies except where western wheat grass thrived. Parts of dormant crowns resumed growth as single or few-stalked plants. The stand at first was open but widespread propagation by rhizomes was rapid and the sod gradually thickened. The greater height, deeper roots, and sod-forming habit of big bluestem placed the bunch-forming prairie dropseed and the low-growing blue grama at great disadvantage; short grass was completely ousted in three years.

Little bluestem was the first major species to decrease greatly in drought; it also suffered the greatest losses and was the last to reappear. Following the drought it was of only intermediate importance and was outranked in abundance by six other dominant species. But flower stalks developed, seed ripened, and seedlings and small tufts were common by 1943. Its return in abundance, often from crowns which had been dormant for 5 to 7 years, in many drought-populated places and in relict areas was spectacular. Differences in relict stands and newly populated areas have been studied.

Bluegrass (*Poa pratensis*) was practically absent by the end of the drought, though formerly it composed about 5 percent of the vegetation. Recovering slowly in ravines it spread upward along them onto the hills. In wetter years it completely covered much bare soil or formed a thin understory to whatever prairie grasses were in possession, except wheat grass, blue grama, and prairie dropseed. It now forms many large patches and often exceeds its predrought abundance. It is important in restoring the soil mulch.

Conditions for growth of seedlings following drought were excellent. In 1943 those of most grasses developed into small bunches. Next year they produced abundant seed and new vegetation flourished. Seedlings of forbs were rare immediately following drought. By 1944 those of certain species were plentiful in places. Reseeding interspaces among the thickening vegetation continued throughout succeeding years.

A good soil mulch occurred everywhere in predrought prairie. Almost none was found on the bare, black soil during the 7 years of drought. By 1944 the denser vegetation had gone far toward reestablishing a protecting cover of debris. Every species contributed to this process but among the more efficient were June grass (*Koeleria cristata*), prairie dropseed, bluegrass, blue grama, side-oats grama, and hairy chess. The mulch was often only partial under needle grass, western wheat grass, and in open stands of the mixed-grass type.

Forbs increased greatly in size three years after the drought, but these were nearly all old plants in the relict bluestem type. Here too they first increased in numbers. Elsewhere societies of forbs were few and highly localized in the more favorable sites. Many species were not found until 1944; some returned even later. By 1945 it was clear that certain species had spread widely and grew abundantly in sites where they did not occur before the grasses had been greatly depleted. In general, the forb population thickened to form societies only slowly. Even seven years after drought the layer of understory vegetation is still far from complete.

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