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THE long period of desiccation, which began in 1934, finally terminated in 1940. The western portion of True Prairie was greatly decimated and a veritable mosaic of types of vegetation resulted. These ranged from well-preserved relict communities of bluestems (*Andropogon*) to mixed stands of grasses on nearly bared soil, but included communities of western wheat grass (*Agropyron smithii*), short grasses (*Bouteloua gracilis* and *Buchloe dactyloides*), needle grass (*Stipa spartea*), and prairie dropseed (*Sporobolus heterolepis*). These types varied in size from a few square rods to many acres (fig. 1). One 15-

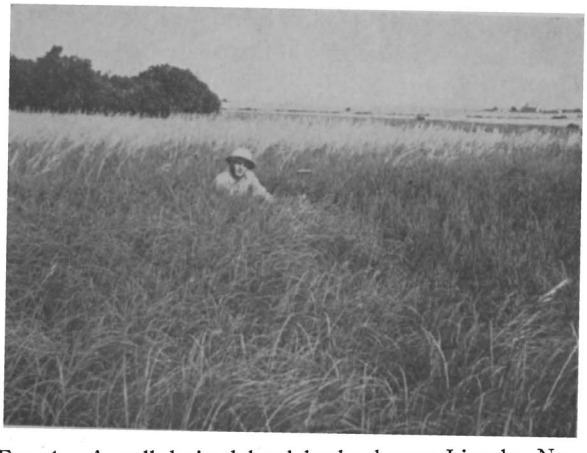


FIG. 1. A well-drained level lowland near Lincoln, Nebraska, formerly completely covered with big bluestem. Relatively small amounts of this type still remain (foreground); western wheat grass invaded the drought-bared soil and formed distinct, pure communities (right center); and the needle grass type (light) developed in the background.

acre prairie, which was mapped in detail, revealed five types, each of which was dominated by a single species, and eight mixed types where two species in each were in definite control. Some of these types of vegetation, moreover, recurred in several parts of this prairie.

Over the entire western margin of True Prairie, wide areas of soil were often still open to invaders in 1940 and others were populated only thinly by individuals of a potential grassland type. Even the vegetation in relict communities had usually been greatly thinned by the drought, and dynamic development involved in mutual invasions, competition, and reaction was pronounced (fig. 2). In this process of revegetation western wheat grass played an important part.

FIG. 2. Former little bluestem prairie which was greatly damaged by drought but naturally reseeded to needle grass, which is now the climax type.

Invasion of western wheat grass into bared soil populated only by early (weedy) stages of the subsere was well advanced during the drought. When good rains came, it continued rapidly along the periphery of its established communities as well as into neighboring ones not yet stabilized. This marginal advance into new territory with a larger supply of water was demarked by greater stature, increased production of foliage, and more numerous flower stalks than in soil already occupied. Under competition for water with wheat grass, relict individuals of nearly all species of grasses and forbs were greatly dwarfed; they often failed to flower, and ultimately succumbed. Hence, wheat grass communities formed remarkably pure stands (fig. 3). Blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*), and under certain

FIG. 3. Portion of a bluestem prairie at Carleton, Nebraska, where the former grasses have been almost completely replaced by western wheat grass.

rainfall distribution side-oats grama (*Bouteloua curtipendula*), alone could successfully adjust themselves to this competition.

Blue grama and its seedlings were so much more drought-resistant than all other species that this grass spread rapidly from relatively small predrought communities even during years of low rainfall. It greatly increased the area of these communities and produced many new ones. After 1940 vegetation was rapidly thickened by the production of new bunches between the old ones and often by the spreading of the stolons of buffalo grass as it recovered under the increased rainfall. The stolons advanced several feet in a single season. They threaded their way among the bunches of blue grama and thus formed a dense sod. Buffalo grass also spread into bared soil and formed a sod. Western wheat grass very successfully invaded communities of blue grama. The rhizomes at first advanced in the bare soil between the bunches or sodded mats but later spread thinly through them. Not only were buffalo grass communities similarly invaded but invasions were also mutual, since seedlings of both short grasses regularly established themselves and later developed an understory to the taller-growing wheat grass. Such a layering of grasses at two levels occurs typically only in mixed prairie (fig. 4). This phenomenon of the formation of mixed prairie by mutual invasion of short grasses and mid grass has occurred over hundreds of square miles. The eastward shift of one major plant community or association into the territory of another association is one of the most striking results of the drought.

Needle grass, characteristic of dry habitats, showed during the dry years a continuous spreading into bared or semibared upland and even onto low ground. The deep planting of the seed and, like wheat grass, early growth in spring were helpful in evading drought. Needle grass formed an important predrought grassland type which has increased in area at least tenfold. The dwarfing effect of needle grass upon neighboring species, while less than that of wheat grass, is still pronounced. The process of thickening its stand, with increase in water supply since the end of the drought, has proceeded so rapidly and the older bunches have become so well established that the climax community has been produced and may remain as such for many generations.

The prairie dropseed, formerly of such small importance that its type held sixth place in predrought True Prairie, has benefited greatly by the death of its competitors and consequent opening of new territory for invasion. Cessation of mowing the prairie, because of very little forage production during the driest years, permitted this late-blooming bunch grass to ripen abundant seed, and its territory has consequently been enormously increased. It has often nearly stabilized its communities almost to the exclusion of other species. Elsewhere more scattered individuals constitute an important component of the mixed type of vegetation.

These several communities occupy most of the

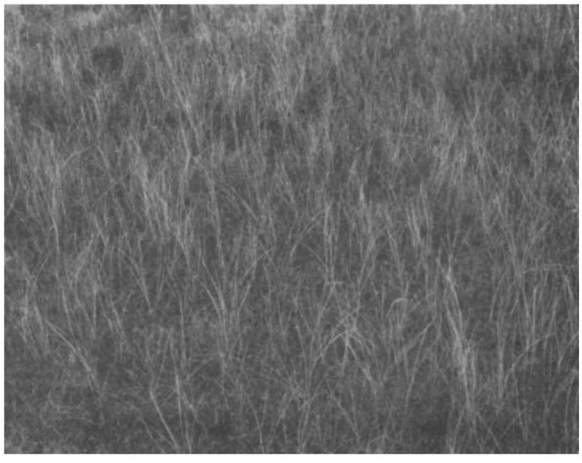


FIG. 4. A thin stand of western wheat grass which has recently invaded an area already occupied by buffalo grass and blue grama and has thus formed mixed prairie.

grassland and stand out clearly like pieces of a mosaic—western wheat grass, blue grama or buffalo grass, mixed prairie, needle grass, prairie dropseed, and relict bluestems. But over considerable areas, widely scattered plants of various species recovered, reseeded, or invaded at about the same time. This gave rise to mixed communities of variable composition. It is here that the battle for dominance will be waged fiercely and probably for a long time. Such mixed communities of needle grass, blue grama, big bluestem (*Andropogon furcatus*), prairie dropseed, tall dropseed (*Sporobolus asper*), and other grasses more or less equally distributed have no place in stabilized True Prairie. With the reseeding of all species since the drought and with vegetative propagation proceeding rapidly, competition has become severe, reactions have become marked, and the nature and manner of stabilization have become a phenomenon of great scientific interest. For it is here that the fitness or unfitness of the species for its habitat, as determined by its reactions and coactions, will be revealed.

Finally, completing the prairie cover are those relict areas where the bluestem grasses were only thinned and not destroyed. These communities, like the preceding, vary greatly in size. They are the portions least disturbed by invasion, although in many cases over 80 percent of little bluestem (*Andropogon scoparius*) succumbed. It was slowly replaced by the rapid spread of big bluestem by rhizomes, by a remarkable increase in side-oats grama, June grass (*Koeleria cristata*), and other native species formerly a part of the community. The process was relatively slow before the end of the drought, but has been accelerated greatly since. Where little bluestem was nearly or completely exterminated, big bluestem sometimes increased from a 10 percent stand to form a pure dense cover (fig. 5).

FIG. 5. An open cover of big bluestem resulting from the death by drought of the more shallowly rooted little bluestem at Carleton, Nebraska.

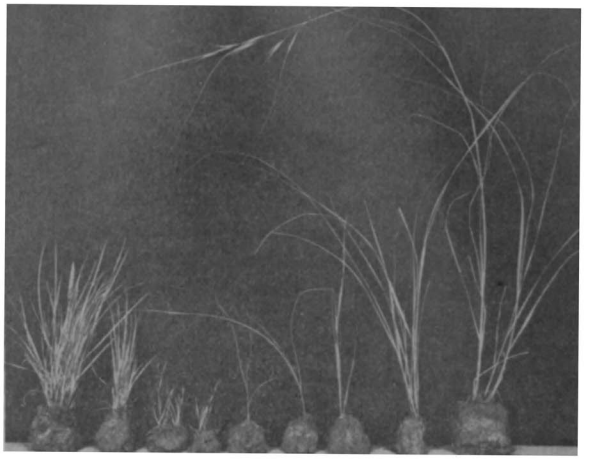


FIG. 6. Various stages in growth of June grass (left) and needle grass (right). The smallest plants are of the current year's growth (samples were taken from the field in June); the largest with flower stalks are completing their third summer of development.

In 1940 much of the prairie was open to invasion, since the cover, except wheat grass, usually presented many open spaces, a square foot to several square feet in area, unoccupied by perennial grasses. These supported a stand of weedy annual grasses or other weeds, or presented a bare surface for seedlings. Debris was not plentiful and the usual thin mulch was not present to protect the soil.

After 1940 seedlings of most species of grasses became common, and were very plentiful by 1943 (fig. 6). Many survived and gradually filled the interspaces everywhere. By tillering profusely, small bunches of grass extended their control over many times that of their predrought basal area. Individual postdrought seedlings grew into bunches several inches in basal diameter. By rhizomes and by stolons the bared spaces were being repopulated by a vigorous vegetation of unusual stature. This increase in development and size was best shown where repopulated denuded areas were adjacent to little-disturbed ones of sod-bound grasses of the same kind which had been neither removed by drought nor succeeded by younger plants.

Corresponding destruction and return of forbs add an interesting part to the process of recovery. Many forbs decreased 50 to 90 percent, others entirely disappeared, but a few increased greatly. Some returned only as seedlings from seed maintained in the soil through the six or seven years of drought. Others grew from rhizomes, root crowns, bulbs, or corms still alive in the soil. Not infrequently the first year's growth from these long-dormant parts consisted of a single small shoot easily mistaken for the stem of a seedling. Revival from dormancy sometimes did not occur until one or more years after good rains came. Some species have not yet returned. Vegetation is usually slow and conservative in its changes.

Restoration of the plant cover is far less advanced toward a complete sod in some portions of True Prairie than in others. This varies with the degree of depletion, the types of vegetation concerned, and with the amount and seasonal distribution of water in the soil. For deficient water content of soil and not temperature or humidity is the chief cause of drought. Availability of water is also the chief condition for recovery. The main patterns of recovery are similar everywhere, but the methods vary greatly with species and season. A new factor has only recently been discovered in great longevity of underground parts of certain grasses.

The uniformity and purity of stands of wheat grass during drought (in the absence of short grasses) have been noted. But only in 1943 —the third summer of good rainfall—have certain wheat grass prairies begun to change to mixed wheat grass–big bluestem by the midsummer appearance of widely spread stems and small clumps of drought relicts. The spark of life remained in parts of these half-decayed root crowns and rhizomes of big bluestem at least five to seven years. Some buds were still in deep dormancy when they were unearthed in July. Little bluestem is likewise putting forth a few culms, most of which are bearing seed, from similarly long-dormant root crowns. Only in coming seasons can one evaluate the importance of this method of recovery on the composition of the climax vegetation.

The present mosaic cover of the prairie, even where complete, is not climax. Only the period of occupation of all the territory has neared completion. Where all available soil is taken, to gain a place in the sun and to receive its portion of water, a newcomer must replace established plants which normally live for many years. This is a slow and difficult procedure. Return to the predrought dynamic equilibrium of climax types will necessitate many changes. If normal precipitation prevails over a sufficiently long period and this return does occur, little bluestem will increase to first rank as regards abundance. The needle grass type will be greatly reduced. Short grasses will almost disappear, and the prairie dropseed type will become infrequent. Wheat grass will be reduced from its present rank of the most important prairie dominant to less than 1 percent of the prairie mixture.

A knowledge of competitive abilities of the various species and how they thrive or wane in mixtures is not only of much scientific importance but also finds immediate practical application. The change from bluestems to wheat grass, for example, at once reduced the value of the grass crop for grazing and hay. Water infiltration has been greatly retarded, water loss by runoff increased, and the excellent structure of normal prairie soil has gradually deteriorated. In True Prairie, cattle graze wheat grass only when better forage is greatly depleted, and it is grazed closely only when other vegetation is absent. Yield of hay in a year of good precipitation (1943) was reduced by invasion of wheat grass in three widely separated upland prairies to 59 percent of that of big bluestem. Comparison of yields were made with big bluestem growing only a few feet distant from the wheat grass. Extensive experiments have shown that water infiltration in soil covered with wheat grass sod was only 42 percent as rapid as its entry into the same kind of soil clothed with big bluestem. Wheat grass is not a desirable species to be employed in alternate husbandry, that is, in rotation of cultivated crops every few years with grass intermixed with legumes, in order to regain good soil structure and to improve fertility by increasing nitrate content and organic matter.

It should be emphasized that the mosaic of grassland patterns at the end of the drought or even after their adjustment during three years of normal rainfall represents only a phase in recovery. Many years with good precipitation will be required to build into the grassland its layered structure, its societies of composites, legumes, and other forbs, and for the less xeric grasses to attain the great abundance and wide distribution characteristic of these dominants under the usual climatic control.

The drought has shown clearly that nature has

richly endowed True Prairie with many species, some of which are best adapted to cover the soil, enrich it, and hold it against the forces of erosion during moist climatic cycles. Others which are then found in such small amounts that they seem almost a non-essential part of grassland rapidly increase to great abundance and become of great importance when a severe drought cycle occurs. This is what happened in the 1934–1940 drought and must have occurred many times in the historical and geological past, although no written record has been made.

After a six-year survey (1928 to 1933) of upland True Prairie of eastern Nebraska and adjacent states, 50 percent of the area was assigned to little bluestem alone. Conversely, western wheat grass was scarcely ever abundant, and side-oats grama and annual fescue (*Festuca octoflora*) occurred sparingly. But when the terrible drought struck suddenly in 1934, little bluestem was nearly swept away, big bluestem and others greatly diminished in abundance, and the soil was nearly bared of vegetation. Nature at once sowed the land with annual fescue, and certain forbs became widely spread weeds in the temporary cover. As if by magic wheat grass covered the land and side-oats grama soon attained second place among prairie grasses. In the dry hot soil, needle grass, prairie dropseed, and other xeric grasses spread widely. In grazed prairie, short grasses migrated eastward and a wave of sand dropseed (*Sporobolus cryptandrus*) swept over the drought-bared land. Thus, it seems that the wide variations in grassland climate are well within the range of endurance of prairie species. Such great changes and adjustments as have been made are among the species of prairie only. Vegetation from neither desert nor forest has been permitted to invade.

In mixed prairie of western Kansas and eastern Colorado, native grassland still occupies about one-half of the area. Practically all of it is used for pasture. These vast range lands are now recovering from the terrible destruction wrought by overgrazing, drought, and dust-burial during the past decade. Grass is man's most powerful ally in soil and water conservation, and pastures are tremendously important as the cheapest and most satisfactory feed for cattle. Hence, the recovery of the western range is not only a phenomenon of outstanding ecological interest but also one of major economic importance. This study is a joint investigation by Dr. F. W. Albertson, of Ft. Hays Kansas State College, and the writer.

The blue grama - buffalo grass type is of greatest extent and importance in western Kansas and eastern Colorado. Hence it received major consideration in a study of the effects of drought, dust, and intensity of grazing on cover and yield of short-grass ranges.

An understanding of present conditions can be had only by a knowledge of past treatment of the ranges. High wind movement was common throughout the drought period and especially severe during the spring of 1935. Soil which had been pulverized by excessive cultivation was carried as dust in large quantities from cultivated fields and deposited in layers or drifts on the drought-stricken prairie plants. The cover of native vegetation was thus greatly reduced, in fact, the grasses were almost or completely annihilated over vast areas of range land. Planted crops failed to grow because of deficient moisture. This compelled the rancher to increase the usual length of the grazing season as well as the intensity of range utilization. This extreme overgrazing was responsible for further decline in the amount of original plant cover. The soil when devoid of native vegetation was often populated by numerous weedy annuals.

The prairie soil was bared by adverse environmental conditions and became extremely susceptible to wind erosion. It was the source of dust for further great storms which greatly damaged the ranges. When pastures were placed under the stress of these unfavorable environmental conditions, it became evident that in those where good management had been practiced the original plant population suffered far less than where overgrazing or overgrazing with intense dusting (a local term meaning covered with dust) had occurred.

At four widely separated stations, Hays, Ness City, Dighton, and Quinter, Kansas, pastures were selected for study at the end of the most severe drought ever recorded. Four classes of pastures were investigated at each station where the range use was known or where records were obtained. Class 1 had been lightly grazed and lightly dusted; class 2 heavily grazed and lightly dusted; class 3 lightly grazed but heavily dusted; and class 4 both heavily grazed and heavily dusted (fig. 7).

Increase in basal area of perennial grasses, amount of the various species concerned, and dry weight of forage produced were the chief

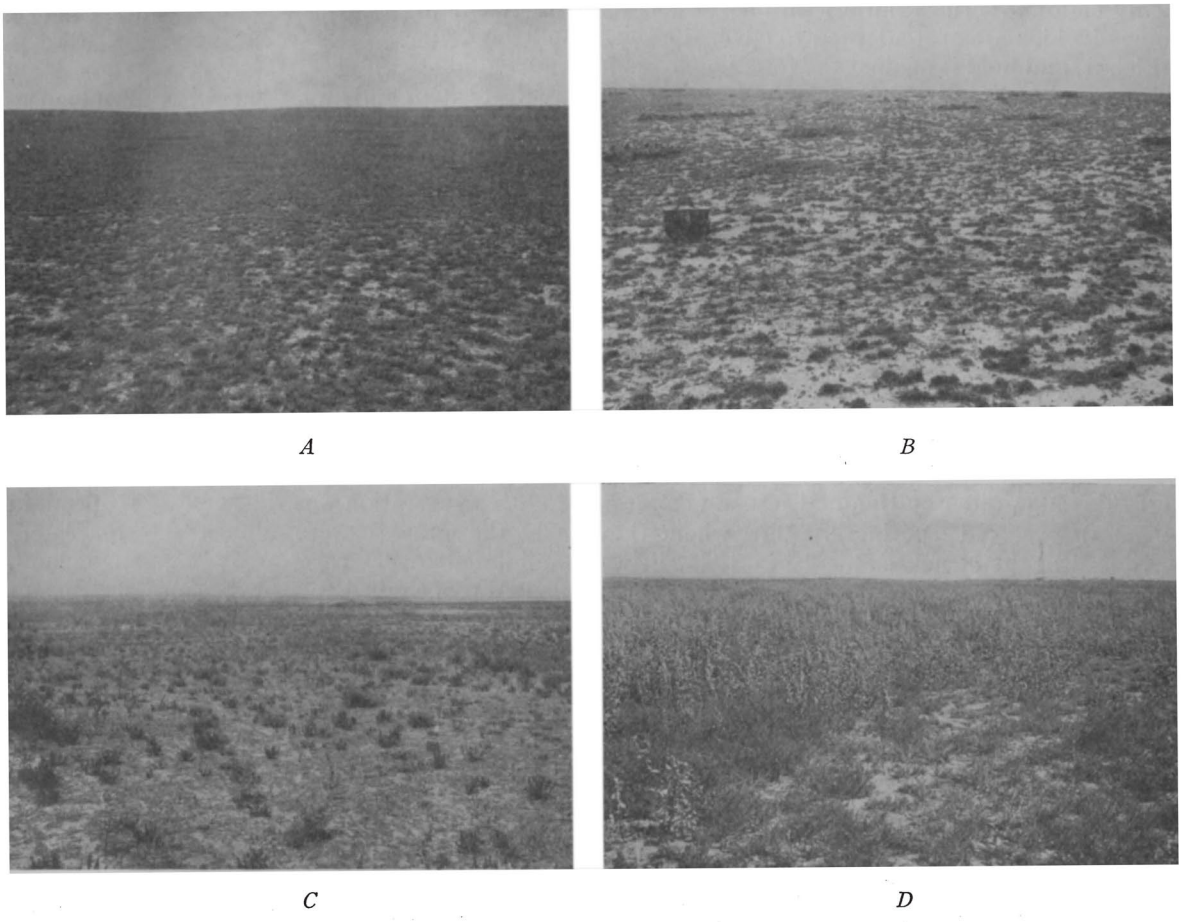


FIG. 7. *A*. Typical view of a class 1 pasture in midwestern Kansas where the open cover remained intact throughout most of the drought. *B*. A class 2 pasture with typical open cover. In early spring such ranges are usually infested with annual weeds. *C*. Class 3 pasture where the original amount of cover has been much reduced and its composition greatly modified. *D*. An overgrazed and heavily dusted (class 4) pasture. Most of the original vegetation died and had been replaced by lamb's quarters, rough pigweed, and sunflower. All photos taken in September, 1940.

criteria used in measuring recovery. Exclosures against stock were made. In each exclosure 20 permanent meter quadrats were clipped annually, and the basal area of the perennial grasses was charted by means of a pantograph in 1940 and 1941. Forbs were so few as to be almost negligible, but annual weeds were abundant. Increase or decrease of basal area of each species of perennial grass was ascertained, and the separate yields of short grasses and weeds were obtained.

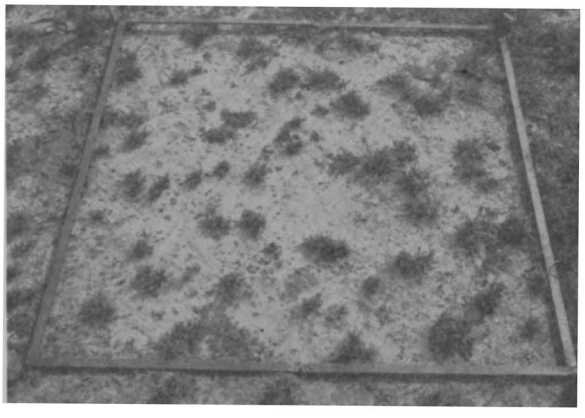
Low precipitation in 1939, 7 to 10 inches below the normal 23 to 25 inches, and an extremely dry fall had further reduced the much depleted plant cover. Drought also weakened the vegetation so greatly that it remained almost dormant at all stations the following spring, and nearly throughout the summer at Dighton and Quinter.

The growing season of 1940 showed much improvement over that of 1939, but precipitation was below normal at all stations during April and June. At Hays and Ness City only was the amount of precipitation normal. Despite the moderate rainfall, the thoroughly dried soil was often without available water at all stations and growth was not continuous and yields were not high, except those of annual weeds.

In 1941 the rainfall was above normal more than half of the time from April to September. The soil was wet from early spring until July; periods without rain were neither prolonged nor severe, and the drought was definitely broken.

Basal area was first ascertained in the fall of 1940 after a year of good recovery, since only then was it possible to separate with certainty

dormant plants from those that were dead. It was invariably least in all class 4 pastures at any station, and nearly always highest in class 1. Cover in pasture classes 2 and 3 was intermediate, but often higher in the lightly grazed but heavily dusted class 3. In fact, a light cover of dust often furnished some protection against drought by aiding dormancy. The average basal cover of short grasses in the four class 1 pastures was 18 percent; that in the others in order was 13.7, 13.4, and 2.2 percent. These percentages are strikingly low compared with the 80 to 95 percent basal cover which was usual before the drought. During the excellent season for growth in 1941 these pastures extended their basal cover to 56.8, 46.3, 44.2, and 17.2 percent, respectively.



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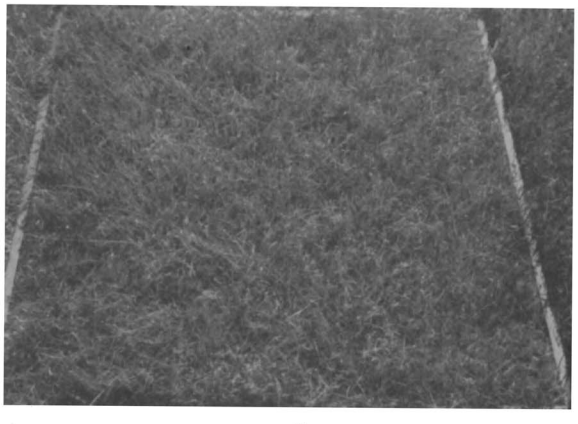

B

FIG. 8. *A*. View of short grass in class 1 pasture at Dighton, Kansas, in the fall of 1940. The basal cover is about 11 percent. *B*. The same quadrat as it appeared early in July, 1942. Buffalo grass had increased greatly and the basal cover was 80 percent.

These results illustrate the wonderful recuperative powers of both blue grama, the most drought-resistant species of the midwest, and buffalo grass, which spreads vegetatively with great rapidity (fig. 8). Although seedling grasses played a very minor role in the process of recovery, yet pasture classes 1 to 3 on an average tripled their cover and basal cover in class 4 increased nearly eightfold.

Blue grama at first exceeded buffalo grass in amount of basal area in all but two class 1 and 2 pastures. But at the end of 1941, buffalo grass exceeded blue grama in seven of these eight pastures. There was about 4.5 times as much buffalo grass as blue grama in the average of class 1 pastures, and about 3 times as much in the average of class 2. In the heavily dusted pastures (classes 3 and 4) in 1940, buffalo grass ranked somewhat higher in all except two, but percentage of cover was low. In 1941, so great were its gains, it ranked far ahead of blue grama, often being 3 to 5 times as abundant. Despite fourfold increases of cover in low-grade pastures, several good years for seed production and growth of seedlings will be required for complete restoration of the range. In many pastures both spread and yield of the perennial grasses were greatly reduced by an abundance of weeds, chiefly little barley (*Hordeum pusillum*), peppergrass (*Lepidium densiflorum*), lamb's quarters (*Chenopodium album*), and Russian thistle (*Salsola pestifer*). They absorbed much water, and greatly reduced the light both when living and when dead. They were most abundant in class 4 pastures. Weeds usually yielded one-fourth ton to more than one ton per acre.

Only broad correlations were found between amount of basal cover and yield. The drought-stricken vegetation varied greatly in vigor; the amount of dust accumulation resulted in varying degrees of dormancy and protection from drought. Moreover, occurrence and amount of soil moisture available to growth were extremely variable.

Previous experience with drought and previous grazing treatments profoundly affected the vigor and future behavior of short grasses, as did also a period of protection. The latter may have been furnished by partial burial by dust. It has been noted that a year of great vegetative activity of buffalo grass, as expressed in abundant stolon production, may be followed by one with much less vegetative increase. Nor is abundant tiller production compatible with the greatest yield of seed of blue grama.