

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Agronomy & Horticulture -- Faculty Publications

Agronomy and Horticulture Department

4-1932

Ecology and Relative Importance of the Dominants of Tall-Grass Prairie

J. E. Weaver

University of Nebraska-Lincoln

T. J. Fitzpatrick

Follow this and additional works at: <https://digitalcommons.unl.edu/agronomyfacpub>



Part of the [Plant Sciences Commons](#)

Weaver, J. E. and Fitzpatrick, T. J., "Ecology and Relative Importance of the Dominants of Tall-Grass Prairie" (1932). *Agronomy & Horticulture -- Faculty Publications*. 429.

<https://digitalcommons.unl.edu/agronomyfacpub/429>

This Article is brought to you for free and open access by the Agronomy and Horticulture Department at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Agronomy & Horticulture -- Faculty Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

THE
BOTANICAL GAZETTE

April 1932

ECOLOGY AND RELATIVE IMPORTANCE OF THE
DOMINANTS OF TALL-GRASS PRAIRIE

J. E. WEAVER AND T. J. FITZPATRICK

(WITH THIRTY FIGURES)

Introduction

This paper is the result of an intensive study of the vegetation of the prairie. The study extended over a period of ten years. It deals with the life histories, distribution, and relative importance of the dominant grasses in a central area of the tall-grass prairie. This area includes the grasslands of the western one-third of Iowa and those of approximately the eastern one-third of Nebraska. On the south it extends into Missouri and Kansas to the Kansas River. Northward it includes a small portion of southwestern Minnesota and a larger one of southeastern South Dakota.

Of the species concerned, all have been grown in experimental plots without competition; under various degrees of competition with other species; and in diverse natural habitats in the prairie. During the past three years 145 individual tracts of prairie have been carefully studied. In addition to the general surveys, hundreds of quadrats have been made in different types of upland and lowland prairies. The grassland areas ranged in size from 15 to 360 acres. They were selected so as to represent typical topography and also to secure rather uniform distribution throughout this vast area of over 60,000 square miles. None of the areas selected was grazed, disturbance being due only to late annual mowing. Just how far this

mowing has modified the original grasslands, which were both grazed and burned, cannot now be determined. But their resistance to invaders, even where the areas are entirely surrounded by them, shows in an impressive manner their high degree of stabilization and their wonderful adjustment to the environment.

Early in the study it was found that roadside observations are often entirely misleading in so far as giving an accurate picture of conditions prevailing in the prairie. Along roadways and in right-of-ways certain species make a good showing. Their conspicuousness and abundance are often such as to lead one to believe that they are really important in the prairie proper. Among such, the most common are *Stipa spartea*, *Elymus canadensis*, *Sporobolus longifolius*, and *Agropyron smithii*. In many cases these are found only sparingly, if at all, in the prairies, although occurring in considerable abundance where even a slight disturbance was made while building the road.

Among the various species of grasses in this centrally located area, the ten following were found to be the most important: *Andropogon furcatus*, *Sorghastrum nutans*, *Spartina michauxiana*, *Panicum virgatum*, and *Elymus canadensis* (all typical of relatively low lands); *Bouteloua racemosa* (of both moist and dry areas); and *Andropogon scoparius*, *Stipa spartea*, *Koeleria cristata*, and *Sporobolus heterolepis* (typical of uplands). It should be understood that upland and lowland are used only as relative terms to designate soils of lower and higher water content respectively. On large, nearly level, upland tracts, grasses demanding a continuously good water supply are found in the depressions. The water content of soil and other environmental factors of the prairie over a period of twelve years have been published elsewhere (6). Here only the development of the grasses based on these determinations will be given. Other herbaceous species will be treated in a subsequent study.

ANDROPOGON FURCATUS

Andropogon furcatus, big bluestem, is one of the two most important dominants of the prairie (fig. 1). Together with *A. scoparius* of uplands, it constitutes fully 70 per cent of the entire grassland cover. It is more mesic than the little bluestem and is best developed

on lower slopes and on well aerated lowlands. It does not thrive in soil that is frequently saturated. Under such conditions it gives way to *Spartina michauxiana*. Almost pure stands, except for a



FIGS. 1, 2.—Fig. 1, *Andropogon furcatus*, about 6 feet tall; fig. 2, *Sorghastrum nutans*

small admixture of *Poa pratensis*, *Sorghastrum nutans*, and a few non-grassy species, occur over extensive areas. A cover of 80-90 per cent of big bluestem is usual on well watered areas. On lower and mid-slopes it not only shares dominance with *A. scoparius*,

but also usually forms 5-25 per cent of the grassy cover on all but the driest hilltops and ridges.

The seedlings develop rapidly when conditions are favorable to growth. In the absence of competition, fine clumps, 12-18 inches tall, may develop in a single growing season and an occasional flower stalk be produced. Usually, however, this is accomplished in the prairie only after three or more years of growth. Winter-killing of the seedlings, and especially of the suppressed ones, is often severe; but after a second year of growth such losses are rather infrequent.

The primary roots develop rapidly. Two months after germination these range from 14 to 40 inches in depth.¹ Many of the roots of the secondary root system spread considerably, often 8-11 inches laterally at a depth of a foot. During the season, even under competition, the roots reach a working level of 2 feet or more. The very abundant roots of mature plants grow both vertically and obliquely downward. A few grow almost horizontally. They thoroughly occupy the soil and form a dense sod. Some roots may extend obliquely from the bunches more than a foot before turning downward. The mature roots are coarse (0.5-3 mm. in diameter) and, although better fitted for absorption than those of *Spartina*, are poorly branched in comparison with those of upland species. Depths of 5-7 feet are usually attained (4).

The tillering habit is pronounced. Seven or eight weeks after germination, tillers begin to appear and soon the seedling develops a small tuft or bunch. Rhizomes are also produced and the area occupied by both shoots and roots is thus greatly increased. The ability of this grass to compete successfully with other lowland species is in large measure due to its rapid development of tillers and rhizomes. Moreover it is very tolerant, especially in the seedling stage, where the leaves remain green and functioning under light values of 5-10 per cent. The lower leaves of plants, two or more years old, also make food under light values of only 10 per cent but only at about one-third the rate of fully lighted leaves.

¹ All data on growth, renewal of activity in spring, etc., are for the central part of the area. Growth in spring starts about seven days earlier on the southern border of the area and approximately ten days later on the northern one, thus making a total difference of more than two weeks.

As a result of the rhizome habit, this grass typically develops a characteristic sod. The individual stems are often spaced about 1 cm. apart. Even in the densest clumps they average less than one per square centimeter. Moreover, between these mats of sod there is much unoccupied soil. The total ground cover in this type rarely exceeds 25 per cent. Notwithstanding this open spacing, the foliage is so dense and the light so greatly reduced that invasion is extremely difficult. It is more or less successfully accomplished by *Poa pratensis*, and easily so owing to annual mowing.

Andropogon, being a genus of southern derivation, renews growth rather late in spring, usually not until the middle of April and several weeks after that of *Poa*. Bluegrass may blossom even before it is much shaded by its big competitor. *Poa* is found in the big bluestem type nearly 80 per cent of the time. It forms 1-15 per cent of the total ground cover. But on the upland, where the tall stems of big bluestem are often too few to reduce the light greatly, invasion is more readily accomplished. In contrast is the very dense sod of *A. scoparius*, where the area actually covered by the plants is rarely invaded.

Development of the shoots in the perennial sod is rapid. By the first of June there are three to five leaves and the average height is normally about 8-16 inches, varying with the habitat. By July 1, the level of the foliage reaches 12-18 inches on upland and 18-34 on low ground. By this time there are one to three dead basal leaves and four to seven large upper ones. The larger leaves have a width of 10-18 mm. and a length of 16 to more than 24 inches. They spread gracefully, so that the area of the top of a clump is usually 1.5 to twice that occupied by the base. The leaves have an osmotic pressure varying with the conditions of aridity of 7.4-14.5 A.²

The flower stalks begin to appear above the general level of the foliage early in July but anthesis does not reach its maximum until in August or September. The height attained by the flower stalks and the number of finger-like racemes produced vary greatly with the season and factors affecting growth, especially the water supply.

² Data on osmotic pressures of the various grasses were kindly furnished by Dr. H. WALTER, of the University of Heidelberg, who worked for a period during the spring and summer of 1930 in the botanical laboratories of the University of Nebraska (3).

On dry slopes flowering may not occur except during very favorable years, when flower stalks only 3 feet tall and with a single pair of racemes are not uncommon. But in the lowland both flower stalks and racemes are extremely abundant and well developed. For example, along the bottom lands of the Missouri River this rank grass reaches a height of 3 feet and the flower stalks 8-10 feet. The latter are woody, have a basal diameter of 5-8 mm., and possess nine to ten leaves. Fifteen or more terminal and axillary racemes are common on an individual stem. Over 200 such flower stalks frequently occur in a single square meter.

The seeds form from late in August until frost. Each is provided with a long, bent, and twisted awn. During late September the foliage begins to dry. The plant then develops the beautiful tints of red and brown or bronze so characteristic of the autumnal landscape.

Big bluestem is an excellent grass to pasture, and also furnishes one of the chief constituents of the "wild" or "prairie hay." It is highly valued as a hay, but must be cut in early bloom or stock will reject it since the stems become too hard and fibrous. On lowlands, where it is best developed, usually two cuttings are made each summer. The new growth rapidly develops and furnishes an abundant second crop.

SORGHASTRUM NUTANS

Sorghastrum nutans, Indian grass, is a tall, coarse species with a water requirement and habit almost identical with those of *Andropogon furcatus* (fig. 2). It is, however, of much less importance. It occurs in greatest abundance in Kansas and southward, but like *Panicum virgatum* it accompanies *Elymus* through the great valleys like the Platte although it is regularly to be found most abundantly in the moister levels. Here it forms clumps of pure sod from a few inches to a few feet in diameter, or, more often, is intermixed with the other lowland species, especially *Andropogon furcatus*. It may constitute 90 per cent of the vegetation where almost pure areas occur in ravines, etc., but this falls to only 5-20 per cent where it is best developed in lowland mixtures. The more usual percentages, however, are 1 to 5 and in many lowlands it is almost absent. Its occurrence in dense, big bluestem sod as isolated stems or very small

clumps is usual. It can easily be distinguished from the latter, which it most closely resembles, by its slightly more erect habit of growth, usually broader leaves, slightly lighter green color, and especially by the very prominent ligules. Where lowlands are occasionally flooded or otherwise disturbed, *Sorghastrum nutans* greatly increases in abundance.

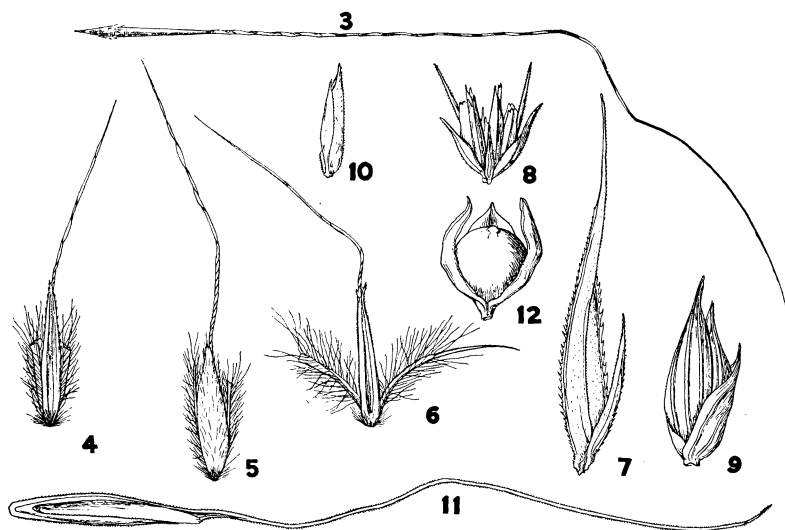
This grass accompanies *Panicum virgatum* and *Andropogon furcatus* up the moist slopes and ravines and is found widely scattered over the broad drainage areas which conduct run-off water. Even on high crests and ridges it may constitute locally 5-25 per cent of the vegetation. Southward it often ranks closely to *A. furcatus* in its importance in upland. Northward it is usually much less abundant and is often almost absent.

The rather large seeds are usually viable and germinate readily unless buried more than half an inch. The seedlings are vigorous and endure a wider range of extremes as regards drought than most lowland species. This probably explains, in part, the habit of this species of readily invading disturbed areas throughout the prairie.

Seedlings develop with marked rapidity, reaching a height of 8-12 inches in three months. Under severe competition, tillering is practically nil, a fact that accounts for the occurrence of single stems of this grass scattered among other species. Where there is little competition three or four tillers and a few short rhizomes are usually to be found by August. Thus single seedlings may soon develop into a small tuft or bunch, or fuse with others into a larger mat of sod. The roots of such seedlings spread widely in all directions to the extent of a foot or more at the 12-inch level. This spreading habit is significant in the competition of seedlings for water in the surface soil. A working level of 18 inches and a maximum penetration of 12-16 inches usually result in an abundant supply of water.

The mature root system reaches a depth of 4-5 feet, which is somewhat less extensive than that of several of the other dominants. However, it is more finely and abundantly branched; hence the plant often succeeds in colonizing dry habitats. Ordinarily a second and sometimes a third season is required for the production of flower stalks, but in moist soil and without competition the life cycle is completed in a single year.

Being of southern derivation this grass begins growth late in spring and ripens its seeds late in autumn. Like big bluestem, it often does not renew growth until after the middle of April, but development is rapid. Within a month the plants may be 10 inches tall and more than twice this height by the first of July. Under favorable conditions the foliage (exclusive of flower stalks) may attain a height of 3.5 feet but it is usually about 2.5-3 feet. The leaves are 8-18 mm. broad and the blades are usually 1-2.5 feet in



FIGS. 3-12.—Fig. 3, fruit of *Stipa spartea*, $\times \frac{3}{2}$; fig. 4, spikelet of *Andropogon furcatus*, $\times 2.5$; fig. 5, spikelet of *Sorghastrum nutans*, $\times 2.5$; fig. 6, spikelet of *A. scoparius*, $\times 2.5$; fig. 7, spikelet of *Spartina michauxiana*, $\times 2.5$; fig. 8, spikelet of *Bouteloua racemosa*, $\times 2.5$; fig. 9, spikelet of *Panicum virgatum*, $\times 5$; fig. 10, floret of *Koeleria cristata*, $\times 5$; fig. 11, floret of *Elymus canadensis*, $\times 5$; fig. 12, fruit of *Sporobolus heterolepis* with attached scales, $\times 5$. All are shown just as they fall from the parent plant.

length. By early summer one or two of the lower leaves are dead and the four or five remaining ones clothe the stem, which is green to the base. The osmotic pressure was found to vary between 8.6 and 11.7 A.

The stems are coarse (3-6 mm. in basal diameter), and even in good stands they average only 4-7 (but sometimes 11-15) per sq. dm. Since there are practically no living basal leaves, more than

90 per cent of the soil surface may be unoccupied; but generally there is a sparse understory of bluegrass and very tolerant forbs. The spread of the tops usually only slightly exceeds twice that of the area occupied by the base, since this species grows rather erect.

Flower stalks begin to appear late in July, and anthesis reaches its height late in August and in September. The large panicles are 4-12 inches long. Since the paniculate inflorescence stands well above the foliage, a total height of 6 to over 9 feet is attained. The seeds, which are disseminated from late in August until winter, are furnished with a bent and twisted awn which is about four times the length of the seed (fig. 5). During September and October the drying leaves give the various shades of yellowish and reddish brown that make the grass conspicuous throughout the winter.

Like big bluestem, this species is an excellent one for grazing and for hay. If cut before the woody flower stalks develop, it is readily eaten by all kinds of stock.

SPARTINA MICHAUXIANA

Spartina michauxiana, tall marsh grass or slough grass, is really not a dominant of low prairie but is the final consociates of the hydrosere leading to the prairie proper (fig. 13). This conclusion is drawn from its successional behavior in the field and from an experimental study of *Spartina* in competition with *Andropogon furcatus* (1, 2). It grows typically in the edge of sluggish streams or ponds and in water-logged or wet soil, rarely occurring in moist soils except in dry seasons or as relicts in soils that have been drained. Its demarcation of soils too wet and consequently too poorly aerated for the growth of maize is clearly shown throughout the prairie. In countless areas the uplands and big bluestem lowlands have been broken, but the slough grass draws and flooded lands were left intact. They are too wet for cropping, at least in spring, but furnish excellent hay, and very successfully hold the soil against erosion. Vast areas of "first bottom" along the Missouri River and its tributaries are covered with *Spartina*, often in almost pure stands. Toward the mesic side it gives way to *Andropogon furcatus*, usually through a transitional zone characterized by *Panicum virgatum* and *Elymus canadensis*. More hydric species of tall sedges, rushes, etc.,

such as *Carex vulpinoidea*, *C. hystricina*, *Scirpus atrovirens*, etc., mark the transition to the earlier reed-swamp stage.

The seeds germinate readily in wet soil, and within a month the seedlings are 2-4 inches high and have developed three or four leaves.



FIGS. 13, 14.—Fig. 13, *Spartina michauxiana*, 6.5 feet tall; fig. 14, *Panicum virgatum* in full bloom, about 5 feet high.

Early in August, even in moderately moist soil, an average height of 12 inches is attained, and by the end of the first summer this is increased to 2.5 feet. The seedlings are not very tolerant of shade.

The lower leaves of suppressed plants die and the upper ones are greatly attenuated; finally the whole plant succumbs. The dominants ordinarily require two or more years' growth before flower stalks are produced. By this time the mature foliage is 3-5 feet high and the photosynthetic surface very great. Because of its tall growth in dense, pure consociations, light values near the soil surface are only 1-3 per cent. Reproduction except in bare areas is undoubtedly almost entirely vegetative.

The rapid development of shoots is paralleled by that of the underground parts. The primary root system elongates at an average rate of nearly 0.5 inch per day, and early in August may reach the 3-foot level. By this time several rhizomes, 2-5 inches long, have developed as well as a good secondary root system. Unlike many upland species, the roots grow almost vertically downward from the plant and its rhizomes and have practically no lateral spread.

Beneath mature plants the surface 6-10 inches of soil is filled with a mat of coarse, woody, very much branched rhizomes, 5-8 mm. in diameter. They vary greatly in length, extending outward 2-15 inches before giving rise to erect shoots. They are covered with long, overlapping leaf scales; the younger ones, especially, are tipped with long, sharp-pointed buds, an adaptation for penetrating heavy, compact soil. The depth of root penetration is surprising, considering the water relations of the habitat. Depths of 8-10 feet are commonly found in wet soil. The coarse, tough roots are 3-5 mm. in diameter and only moderately well branched. In fact, this grass has coarser roots than any of those of the prairie proper (5). When grown in drier soil, branching becomes much more profuse. Blocks of *Spartina* sod when transplanted to high upland developed profusely branched roots 11 feet long and persisted, producing short flower stalks on wet years, for a period of ten years.

Although this species renews activity rather late, often not until the second week in April, it grows more rapidly than any of the grasses of the prairie. By the first of June it is frequently in the fifth- or sixth-leaf stage and varies from 2 to over 3 feet in height. Where it shares marginal areas with *Panicum virgatum* or *Andropogon furcatus*, it conspicuously overtops them. The general height of

the leaves at the end of the growing season varies from 3 to 7 feet, depending upon the water supply. Because of the extensive rhizomes this species always forms a sod. Where best developed, the coarse woody stems, which are 2-10 mm. in diameter, are widely spaced. In the densest cover there is usually only one stem for every 3-20 sq. cm. of soil surface, and the surface actually occupied is often only 1-3 per cent.

Where an abundant and constant water supply favors the growth of *Spartina*, other grasses are effectually excluded. Although often in groups of three or more, the stems are more usually singly spaced and the cover is uniform. The shade is dense. Two or three of the basal leaves are generally dead by midsummer, leaving the stems bare to a height of about 8-12 inches. The six or seven living leaves, where water is plentiful, are sometimes 15-18 mm. in width and 2.5-5.5 feet in length. The osmotic pressure of the leaves varied from 11.4 A. in early summer to 16.4 during a September drought. These determinations, however, were made on relict plants in low prairie.

Even in moist soil the flower stalks are 5-6 feet tall and in wet areas often reach 9-10 feet. Flowering begins about the second week in July, but the height of anthesis occurs approximately a month later. Flowering may continue until frost. The large, conspicuous panicles are 12-24 inches long and 6-10 inches wide.

Slough grass makes good hay if it is cut before the woody stems are much developed. The common practice is to mow the sloughs about three times each year. Since growth is quickly renewed and very rapid, heavy yields are thus assured. Slough grass is also used for thatching sheds and covering hay stacks.

PANICUM VIRGATUM

Panicum virgatum, tall panic grass, a tall, coarse, rank, sod-forming grass, is an important dominant of low, moist soil (fig. 14). It has migrated far up ravines and draws and also occurs in disturbed areas in uplands. It is more important in the southern and eastern portions of the area where the climate is more humid as well as warmer. It is perhaps the most mesic of prairie grasses, as is shown by its abundance in the drier portions of the *Spartina* consociates, occupying with *Elymus canadensis*, *Agrostis alba*, etc., areas that

are too poorly aerated for the big bluestem. It is rarely found in extensive pure stands, the clumps and areas usually alternating with *Spartina*, *Carex vulpinoidea*, etc. In such mixtures it covers many square miles of poorly drained bottomlands along the Missouri and its tributaries, constituting 10-30 or more per cent of the vegetation.

Tall panic grass is almost invariably found as a transitional species along ravines and draws wherever big bluestem gives way to *Spartina michauxiana* (or southward to *Tripsacum dactyloides*). The transition, whether gradual or abrupt, is characterized by small patches of dense pure stands, by clumps often 3-4 feet in diameter, and by an intermingling with the bluestem on its marginal areas. While *Panicum* may locally constitute 25 per cent of the grass mixture, this often falls to 10 per cent, and, where big bluestem is well developed, to less than 3 per cent.

Panicum is found in areas of higher water content along draws and the broad sloping flats receiving run-off water at the heads of draws. The rank growth at the bottom of ravines, where it is often 5 feet high, gradually decreases to about 3 feet near the top. Moreover the exclusive, dense sod becomes thinner as the grass extends its area into drier lands, often a rod or two on the sides of the draw, until only scattered, dwarfed individual stems one to several inches apart occur. On the uplands it secures a foothold in areas of greater water content, where disturbance has occurred. Here it is found widely scattered in small clumps or as isolated individuals, and is of no importance in the percentage composition of the cover of vegetation.

Seeds of this species usually give a low rate of germination and propagation is undoubtedly largely by rhizomes. The seedlings develop rapidly. Unless competition is too severe, tillering and rhizome production begin in five to seven weeks. Where the light is reduced to 5-10 per cent, near the soil surface, suppressed plants make food at only one-half the rate of dominant seedlings. This species appears to be less tolerant than big bluestem. Seedlings persist for two years, however, in disturbed areas occupied by dense growths of coarse herbs, such as *Oenothera biennis*, under a light intensity of 12-20 per cent, and take complete possession of the area upon the disappearance of the herbs.

Three months after germination, heights of 12-20 inches are attained. By this time a typical seedling possesses two or three tillers, two to four rhizomes, some half an inch in length, and a good root system 12-30 inches deep. This species, however, does not tiller as readily or as abundantly as big bluestem, and in addition the mortality of seedlings due to winter-killing is often very great.

Unlike the vertical roots of *Spartina*, those of *Panicum* spread 5-6 inches in all directions when only 6 inches deep. The roots are extensive but very coarse, and lack the profuse network of branches characteristic of upland grasses (fig. 15). They may attain a depth

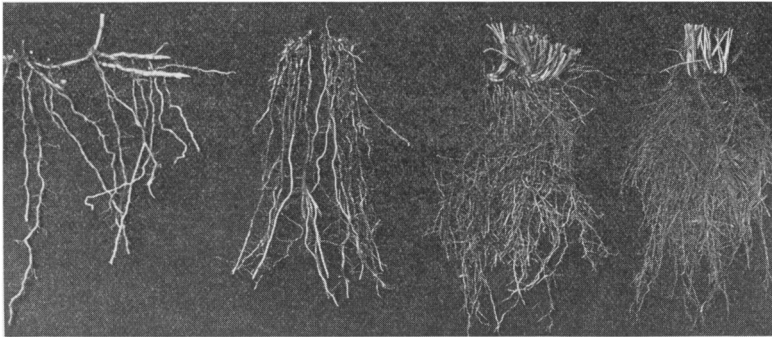


FIG. 15.—Portions of root systems of *Panicum virgatum* (left), *Andropogon furcatus*, *A. scoparius*, and *Koeleria cristata* (right), showing the much finer roots of the two upland species.

of 5 feet in a single summer. Under favorable conditions the root system may more than double in length during the second season, the foliage reach a height of 3 or more feet, and flower stalks be produced.

The mature root system is the longest of any of the grasses of the prairie. The roots are very coarse, many being 3 or 4 mm. in diameter. They pursue a vertically downward direction, spreading only a little near the surface, to a maximum depth of more than 9 feet.

Since this species is of tropical derivation it renews growth late in spring, often about April 20. Owing to an abundant food supply in roots and rhizomes, it grows rapidly, and by June 1 is 18 inches high and in the third- or fourth-leaf stage. It is always distinctly taller than the big bluestem. Where mowing or fire does not remove it, the accumulated débris is often 7-10 inches thick the following

spring. This receives the insolation rather than the soil and results in a colder habitat which delays growth. After two years' accumulations such a cover is decidedly harmful and tends to reduce the stand.

The height attained by mature plants varies greatly with season and water content. On uplands it is often 3-3.5 feet; in wet lowlands a maximum height of 4.5-6 feet is attained. Fully developed plants in close stands usually have one to three dead basal leaves and six or seven living ones, all on the coarse, woody stems which are 2-5 mm. thick. The flat leaves are 14-24 inches long and 8-14 mm. wide, thus presenting a large photosynthetic surface. They reduce the area by rolling during dry weather. An osmotic pressure of 13.7 A. has been determined for this species during a period of drought. As with the preceding grasses, nearly full height of the vegetation is attained by the middle of July. Then large, open, spreading panicles, which become 12-20 inches long and 16-20 inches wide, begin to appear. Flowering begins in July, reaches a maximum in August, and continues until frost in late September or October. The seeds are shed in late fall and winter.

Owing to the lack of basal shoots and the wide spacing between the unbranched stems, only a small amount of the surface soil is actually occupied. In good stands only 4 to 24 stems occur per sq. dm. and 90-95 per cent of the ground is bare. *Poa pratensis* and various carices often occur as interstitial species, but usually sparingly because of the low light intensity. Their roots absorb from the soil occupied by the dense mats of coarse rhizomes and roots of the tall grasses. In regard to the light relation also, *Panicum* has much the advantage.

This grass affords good grazing when young, but as the stems become lignified forage value greatly decreases. Stock, however, eat the panicles and leaves even of mature plants. It is excellent for hay, and when cut before the stems become woody (usually twice per summer) it gives large yields.

ELYMUS CANADENSIS

Elymus canadensis, nodding wild rye, is also a tall, coarse grass of high water requirement (fig. 16). Although of wide and regular distribution, over the prairie as a whole it is a dominant of minor

importance. It is typically a lowland species, reaching its best development in the wet transitional areas between *Spartina michauxiana* and *Andropogon furcatus*. It also intermingles more or less with both of these. On uplands it is found usually only where local disturb-



FIGS. 16, 17.—Fig. 16, characteristic clump of *Elymus canadensis*, about 5.5 feet high; fig. 17, large clump of *Bouteloua racemosa*. Flower stalks about 3 feet tall.

ances, such as gopher mounds, badger holes, etc., have occurred. With *Panicum virgatum* it forms a reliable indicator on upper slopes and ridges of increased water content due to local denudation. Once in possession the bunches or clumps may remain for many years.

The persistence of a species when once established is worth careful consideration. Possession by long-lived species is the law in grassland. For example, clumps of *Elymus*, *Panicum*, and *Spartina* transplanted to the crest of a dry hill among upland grasses, such as *Stipa*, *Koeleria*, etc., have persisted, some for ten years. They have rooted deeply, *Panicum* and *Spartina* to 11 feet. Although unable to extend their areas, during wet years they put forth flower stalks and blossom.

Elymus occurs only in isolated clumps in uplands, and even on lowlands it forms pure stands only in very local areas. Usually it constitutes a 1-5 per cent mixture among the other grasses and exceptionally 10-15 per cent. Northward and westward it becomes more abundant than in the south and east. On level land subject to overflow, and too wet for big bluestem, it often covers large tracts resembling thinly planted fields of barley. Examination shows that the abundance is more apparent than real. Rarely more than 40 to 50 stalks occur per square meter. Since during midsummer there are few or no basal shoots or leaves, this grass may form only 5-8 per cent of the ground cover.

The relatively large seeds show a high rate of germination as determined by experiments extending over a period of ten years. Unlike most grasses, even when the seeds are covered with soil to a depth of 1-2 inches they still produce seedlings abundantly. Within a month the plants are 2-3 inches tall and in the third-leaf stage. Early in August a height of 6-10 inches is attained. Where grown without competition (as in locally denuded areas) it often exceeds a foot in height, and sometimes produces small flower stalks the first season. Flower stalks are developed the second year even under close competition. Because of its northern derivation, seedlings do not badly winter-kill.

Development of the underground parts also takes place rapidly. After three months' growth, the well developed and widely spreading roots reach a working level of 18 inches and a depth of 25-30 inches. Although the primary laterals seldom exceed 2 inches in length, they are branched to the third and fourth degree.

Tillering begins early, only four or five weeks after germination. By midsummer all but suppressed seedlings have one to three tillers

each. The short rhizomes result in the formation of bunches or clumps.

The roots of mature plants seldom exceed 2.5 feet in depth and are thus much shallower than other lowland dominants. The obliquely running roots may spread nearly 2 feet on all sides of the plant, however, and the roots are more finely branched than those of the other lowland dominants, with the possible exception of *Sorghastrum nutans*.

Growth is resumed very early in spring. Late in March new shoots are frequently 3-5 inches long and bear several green leaves. This takes place before *Panicum virgatum*, *Sorghastrum nutans*, and other tall-grass competitors have renewed growth, giving *Elymus* a great advantage in competition, especially for light.

Elymus reaches a height of 30-40 inches by the middle of June, and soon the spikes begin to appear. These are 6-9 inches long and often 1 inch in diameter, including the awns. The stout, rather woody stems are 3-5 mm. thick. They usually occur in loose clumps or are widely spaced in a more or less continuous, open sod. They usually have one or more withered leaves and seven to eight green ones. The flat leaves are 10-20 mm. wide but only 8-15 inches long. The osmotic concentration of the cell sap of the leaves ranged from 13.0 A. in spring to 19.1 A. during severe drought. A period of maximum blooming occurs during July. During the ripening of the seeds the spikes bend over gracefully, which accounts for the very appropriate name, nodding wild rye.

Elymus is a good forage grass, and when cut early furnishes an excellent component of "prairie hay." If mowed late the stems are woody and the heads are often infested with ergot.

BOUTELOUA RACEMOSA

Bouteloua racemosa, side-oat grama, is scattered widely throughout the prairie in all types of situations, but rarely occurs in great abundance. The largest undisturbed area found that was controlled by this tall grass did not exceed a few square meters. It nearly always occurs as small, isolated, rather open tufts scattered among the other species, especially in the *Andropogon furcatus* type of prairie (fig. 17). A 1-3 per cent mixture is common, even on uplands, and

it may occur as abundantly as 10 per cent locally. Its habit approaches that of an interstitial species, and where there is disturbance, such as is caused by erosion on steep banks, etc., it frequently increases in abundance. Quadrats in old roads along ridges sometimes give an abundance ranging from 15 to 60 per cent. It withstands grazing rather well and increases in territory under moderate pasturing. Although nearly always represented in any considerable area, its importance is not great.

The seeds are usually viable and give a good rate of germination even when buried an inch in the soil. The seedlings make an excellent growth and tiller vigorously. In a bare area, for example, the seedlings were 11 inches tall by July 30, when the roots had reached a working level of 18 inches and a maximum depth of about 3 feet. The plants bore seven or eight tillers, fifteen roots, and one or two rhizomes. Even at a foot in depth the laterals were sometimes 9 inches long, and spread widely through the upper levels of the soil. By October, flower stalks 1.5 feet tall were abundant and a large crop of seed was produced. Under competition, however, rate of growth is much reduced and blossoming ordinarily does not occur until the second or third summer.

Its tall stature and excellent absorbing system, together with its tolerance of shade, enable this species to compete more or less successfully for a place in the sod.

This *Bouteloua* renews growth late in April at about the same time as the bluestems. It grows rapidly, reaching a height of 3-3.5 feet and a depth of 5-6 feet. Tillers arise abundantly from the numerous short rhizomes and the spreading base of the plant is well clothed with rather short leaves. The unbranched stems have five to seven leaves each, which are progressively shorter from the second one to the top. The leaves vary in length from 4 to 14 or more inches and are about 5-7 mm. wide. An osmotic pressure of 12.6 A. has been found during midsummer. The dry, curled, whitish, rather hairy basal leaves are characteristic and readily mark this species in the vegetative state.

Flower stalks begin to appear about the first week in July and anthesis continues through August and September. The racemes are 6-12 inches long and have anywhere from 25 to 50 spikes, all usually

hanging gracefully from one side. Even when all the spikelets have fallen, the species is readily identified by the zigzag rachis.

This grass furnishes nutritious forage for all kinds of stock, and is readily eaten at all times, even in the dormant condition. It furnishes a minor constituent of the hay from the prairie.

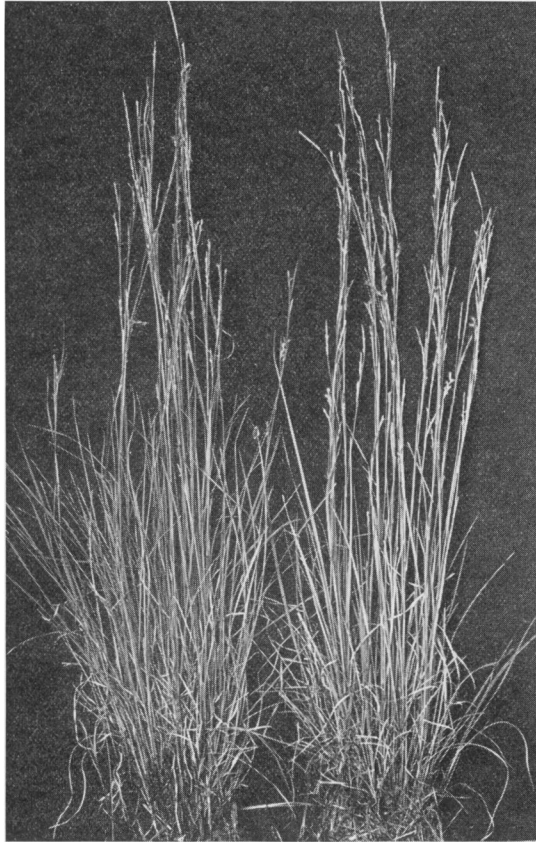


FIG. 18.—Characteristic bunches of *Andropogon scoparius*, showing leaves about 15 inches tall and mature flower stalks.

ANDROPOGON SCOPARIUS

Just as *Andropogon furcatus* is the most important dominant of low prairies, so also *Andropogon scoparius*, little bluestem, forms the great bulk of the upland grass cover (fig. 18). It easily exceeds

in importance all of the other upland species combined. In the south and east, where moisture is more plentiful, its chief competitor is big bluestem. In the north and west, especially on poor soils and areas with extreme run-off, it is intermingled with *Stipa spartea*, which sometimes replaces it in local areas.

This species ordinarily forms a much interrupted sod, best developed northward, in which the mats or tufts are so dense that few other species can invade them. Accompanying species grow between the mats or bunches. Where the slopes are steep and the run-off and erosion are great the bunch habit becomes pronounced.

On the deep soils of the steep, drier, loess hills, this species alone frequently constitutes 90 per cent of the vegetation, and in drier soils as a whole, including level uplands, 50 to 75 per cent. On mid-slopes and lower hillsides it forms alternates or more usually intermingles with the big bluestem, often on equal terms. On lower lands the big bluestem and other taller grasses have the decided advantage in securing light, and if there is sufficient water for a continuous cover of the taller grasses, little bluestem entirely disappears.

The percentage of germination is often low but the seedlings are vigorous. During the first summer they reach a height of 6-8 inches and tiller profusely. For example, seedlings in late July were 5.5 inches tall. They had developed three or four tillers and eight roots each. The latter reached a working level of 12 inches and a maximum depth of 18 inches. The young roots are fine and extremely well branched, some of the branches attaining lengths of 3-4 inches. Thus the plant is well fitted to absorb in relatively dry soil. In the absence of competition it may complete its life cycle by producing flower stalks and seeds the first year; but in the prairie, this requires two seasons very favorable to growth, and ordinarily three or more. The mature root system consists of a vast network of threadlike roots and masses of finely branched rootlets, some over 30 inches long. Thus the soil beneath the sod and several inches on all sides of it is filled with a dense mat of roots to a depth of about 5 feet. Such an absorbing system is remarkably efficient.

The leafy stems grow compactly in the sod mat. Even where poorly developed, 50-80 stems occur per sq dm. and there are often 100-300 crowded into a similar area. Many of these are furnished

with several tillers each and all are leafy to the base. Thus the mat is compact and there is little room for invasion. The density of the mat varies with the water relation and also with age. On lower slopes and in areas of greater rainfall the whole sod may consist of closely crowded stems, but on uplands during dry years the center may have few stems and the peripheral ones show a markedly better growth. Deterioration of the clump nearly always occurs first in the older, central part and proceeds toward the periphery. The leaves are usually only 3-4 mm. in width and 4-8 inches long, but sometimes measure as much as 18 inches. Usually only the three or four uppermost ones are green and one to three dried, dead ones clothe the base of the stem. Where the grass is not mowed, the dead leaves intermingle with the living ones to a height of about 7 inches. An osmotic pressure of 7.9-30.4 A. has been determined for the foliage.

The size of the sod mats is variable. In favorable situations solid clumps 1.5 by 2 feet in extent may be found; but normally they are smaller, often 6-8 inches or less, and rather irregular in shape. Often the sod consists of smaller tufts rather closely aggregated, so that the overlapping leaves give an apparent cover of 80-100 per cent; actually the basal cover in any case seldom exceeds 25 per cent. Larger and better filled clumps occur southward, while the best development of the tufted sod-mat type is frequently found in northern Nebraska and Dakota. When the foliage is well developed, the spread of tops is often approximately twice that of the basal area. The height attained by this species is variable. It ranges from 7 to 10 inches on dry hilltops and regions of lowest rainfall to 20 inches in the warmer, more humid regions southeastward. On moderately low lands, in competition with the taller grasses, the leaves attain heights of 2-3.5 feet.

Growth begins in late spring, often about April 15, and at a time when *Stipa spartea* and *Koeleria cristata* have well developed bunches. Flower stalks begin to appear by the middle of July and are abundant late in August. The inflorescence consists of a single raceme from each peduncle. These are terminal both from the main stalk and its branches. The raceme is loose and usually 1-2.5 inches long. The flower stalks vary from 1.5 to 2 feet high on dry uplands,

where blossoming may occur only in exceptionally wet years, to 3-4 feet under a more favorable water supply. Flower stalks are usually thickly grouped and seeds are produced in great abundance. Each has a twisted awn about 0.5 inch in length (fig. 6). By early winter nearly all the seeds have been dislodged by the wind, but the old flower stalks persist for a long time. The beautiful autumnal coloration of upland prairie is largely due to the various shades of yellows, reds, and bronze afforded by the drying plants of this species.

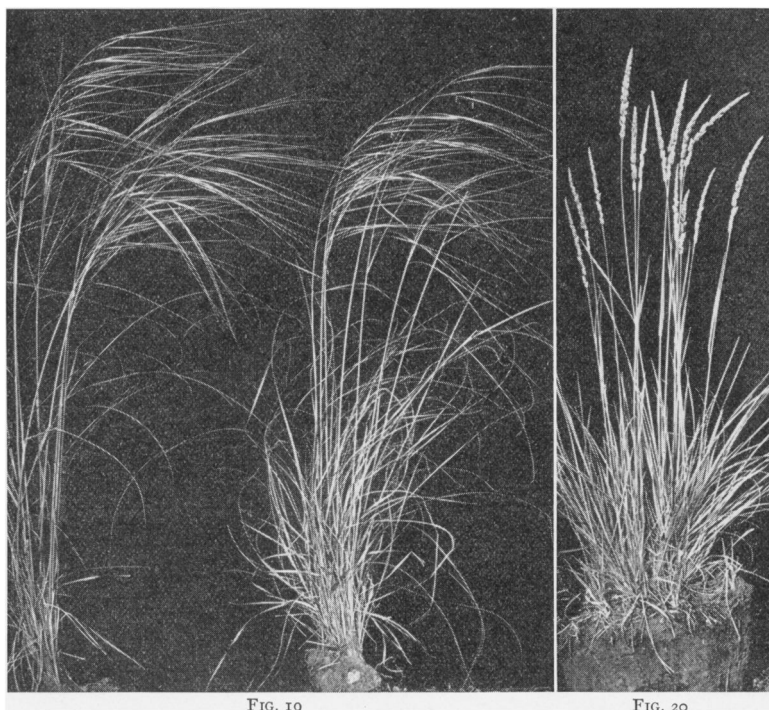
Little bluestem is a rather good forage grass and furnishes satisfactory grazing when the dry stems do not interfere. It is a chief constituent of hay from upland prairie, and is best when cut early.

STIPA SPARTEA

Stipa spartea, needle grass, is typically an upland species (fig. 19). It is practically of no importance in the portion of the area in Kansas and Missouri, but gradually increases in abundance and is an important species of the prairie northward. Steep, dry ridges and xeric slopes, especially where the soil is thin and perhaps sandy or gravelly, are frequently more or less dominated by *Stipa*. Such areas alternate with *Andropogon scoparius* or *Sporobolus heterolepis* (to be described), or even with a more or less equal mixture of the bluestems. Its chief associates are *Koeleria cristata* and little bluestem, but it is found in various grassy mixtures.

Because of its excellent growth on dry banks along roadsides and its very deceptive appearance as regards abundance, its frequency and importance are easily overestimated. Even where the bunches are a foot apart, the widely spreading leaves and gracefully bending stems, which may extend 1-3 feet on all sides of the clump, give the appearance of a thick growth. A study of the composition of the vegetation in which *Stipa* appears to dominate shows that it often constitutes only 15-35 per cent of the prairie. Rarely does it comprise 50-80 per cent of the plant cover and this only in local areas. In many prairies it is scarcely represented; usually it forms 1-5 per cent of the vegetation as a whole; but in hilly lands in the central and northern parts of the area alternates of *Stipa* may cover from one-fifth to one-third or even more of extensive uplands. Moreover, it is

frequently more or less abundant on flat lands at the heads of draws, and is readily distributed over broad washes on lower slopes that are subject to overflow and deposit during exceptionally heavy rains. Here it is found with big bluestem, usually in no great abundance, but sometimes dominating rather extensive local areas.



FIGS. 19, 20.—Fig. 19, bunches of *Stipa spartea* with fruits maturing, height about 3 feet; fig. 20, *Koeleria cristata*, just after blooming, flower stalks 2 feet high. (Photographed June 15, 1931.)

The large, heavy seed in the long-awned fruit germinates usually only after being worked 1–3 inches into the soil. The seedlings make a good growth and by midsummer the parent culms are often 8–12 inches tall and possess five leaves and three or four tillers. By this time the fine, well branched root system is usually 15–20 inches deep and in good contact with the moist subsoil. True to its boreal extraction, year-old *Stipa* seedlings begin growth in March. They are

4-6 inches tall and are in the third- or fourth-leaf stage before most other grasses have broken their dormancy. By the second summer the foliage may reach a height of 2 feet, but flower-stalk production ordinarily does not occur until the third year. The root system of even mature plants seldom reaches a depth greater than 2.5-3 feet, but it is exceedingly well fitted for absorption in the upper soil levels. Numerous, profusely branched, smaller roots fill this region, and the larger ones give rise to many laterals which divide into fine branches in the deeper soil.

The production of tillers and short rhizomes gives rise to more or less circular clumps or bunches; this species never forms a sod. The size of the clumps is variable depending upon conditions of growth; some are only 1 cm. in diameter, the largest perhaps 12 by 12 cm. A very usual size under ordinary conditions is 3 by 5 cm. The bases of long, spreading clusters of rosette-like leaves remain partly green during the winter, although the distal two-thirds' portions of the leaves are usually frozen. Growth begins with the first warm days and the foliage is often 2 feet high by the first of June. At this time flower stalks are well developed.

The flower stalks are from 2 to 4 feet tall. Tufts 1 or 2 cm. in diameter may have only one or two flower stalks, but large clumps in more favorable areas may produce 18 or more. During dry springs seed production is greatly reduced.

The height of the foliage varies from 14 to 36 inches, depending upon the degree of competition and the amount of available water. The somewhat glaucous, rather stiff, deeply ridged leaves are only 3-4 mm. wide but 1.5-3 feet or more long. The long attenuated ends are mostly dead and dry. There are usually only three living cauline leaves and one or two dead ones. The ligules are prominent. An osmotic pressure of cell sap of 12.7-24.4 A. has been determined.

By June 10 the twisting awns, which are 4-6 inches long, indicate the ripening of the seed. Usually by the first week in July the seeds have all fallen and are widely scattered by the wind. The fruit is buried in the soil by the torsion of the bent and twisted awn, which is held from turning by the bases of the grass stems. This excellent method of planting the seed compensates for the small number, which ordinarily ranges from 12 to 25 for each robust flower

stalk. Even after the seeds have fallen, the persistent, broad, drying scales (3-4 cm. long) on the spikelets glisten in the sun so that the whole hillside, where the plant is at all abundant, has a silvery appearance.

Wherever *Stipa* is thick, the ground cover is very open, and the greater the apparent density of the species the barer the soil. For example, in quadrats with 25-35 bunches of moderate size only 5-7 per cent of the surface soil was occupied. Where the number drops to 8 or less per sq. m. other grasses occur more abundantly and the total cover correspondingly increases. These relations hold on even relatively low land.

In general, *Stipa*, with *Koeleria cristata* and *Sporobolus heterolepis*, occurs on more immature soils and thus represents an earlier stage in development than do the species of *Andropogon*. The ability of *Stipa*, especially, to colonize thin soils and disturbed areas is due partly to its excellent method of deeply planting the seeds in contact with moist soil; partly to its excellent and rapidly developed root system; and partly to its early growth, by means of which it avoids excessive competition. The last, however, is detrimental under grazing and explains why *Stipa* is among the first grasses to disappear. Animals feed on it at a time when the other upland grasses have commenced little or no growth. Such grazing greatly decreases growth, limits seed production, and may result in the disappearance of the species.

KOELERIA CRISTATA

Koeleria cristata, June grass, is a bunch grass but of smaller stature than any of the preceding (fig. 20). Like *Stipa*, it is of boreal origin and is abundant in the northern part of the area. It shows a decided preference for dry uplands and is typically associated with *Stipa spartea*, *Sporobolus heterolepis*, and *Andropogon scoparius*. Not infrequently, however, it occurs also on lower mid-slopes as well as on well drained lowlands.

The necessity of good aeration for upland species and the greater tolerance of those of lowland to deficient soil air resulting from high water content are well illustrated in the following experiment.

Late in April large blocks of sod were removed to a depth of about 8 inches and transplanted into a *Spartina* swamp. These

blocks contained all of the more important prairie species and also included *Spartina michauxiana*. The last was dug up and replanted in its native habitat. The soil was completely saturated until about June 15 and a high water content prevailed throughout the summer.

By the first of June *Andropogon scoparius* died; most of the leaves were dead on *Koeleria*; and all of the upland species, especially, showed by wilting and dead leaves the harmful effect of deficient aeration. The middle of June found *Bouteloua racemosa* dead; *Stipa* had almost succumbed; the flower stalks of *Koeleria* had rotted to the base, and only a few green leaves remained. A month later both *Koeleria* and *Stipa* had died, thus completing the mortality of upland species.

The species native to low prairie did much better, although those requiring the most aeration (*Andropogon furcatus* and *Sorghastrum nutans*) died by the end of summer. *Elymus canadensis* lost most of its leaves and the flower stalks completely decayed at the ground line, but it sent forth new basal shoots. *Panicum virgatum* and *Spartina* grew very well, the latter flowering in a normal way. The swamp was somewhat drier the following year and all three of these lowland species became firmly established.

In many prairies, especially southward, *Koeleria* may be scarcely if at all represented; but it more usually forms 1-3 per cent of the cover, at least locally. An abundance greater than 5-10 per cent has rarely been found except in disturbed places. The small tufts are widely distributed, however, and upon close inspection isolated plants may frequently be seen.

The seeds are produced in great abundance and usually give an excellent germination. The seedlings have much more difficulty in becoming established than those of most prairie grasses. During summer drought the mortality is always high and many are also winter-killed.

The dominant seedlings tiller freely and soon a small clump is formed, the plants often reaching 3-8 inches in height the first season. Usually two or three years are required for the production of flower stalks.

The root system is relatively shallow (15-28 inches) but fine and exceedingly well developed. A great network of fine rootlets spreads

outward from the base and occupies the soil to a distance of 8 inches on all sides of the plant, some absorbing within 0.5 inch of the soil surface. It may be, as in the case of *Stipa*, that the early growth in spring and rapid maturity of this species are correlated with the shallow root system.

Koeleria makes an excellent growth after the fall rains and remains green after most of the grasses have dried. With the first days of spring, growth is renewed vigorously and then the green clumps are conspicuous against the background of dead foliage. By the end of May the foliage is often 12-15 inches tall and flower stalks are developing.

The tufted sods vary from 1 to 12 cm. in width, 4 by 5 cm. being an approximate average size. While the smaller clumps have only a few leaves and a single flower stalk, larger ones have an abundant foliage and 20 to 30 stems. In the best stands in the prairie, 15-50 tufts may occur per sq. m., varying in size from single plants to bunches with 10 to 30 stalks. In disturbed areas as many as 80 fruiting heads have been counted in a single clump. In such places, usually as a result of repeated burning, June grass may appear like a thin stand of timothy, but the actual ground cover where it is thickest rarely exceeds 16 per cent. Since this species grows rather erect, the spread of tops is only 1.5 to twice that of the base.

The soft, pliable leaves of this grass are mainly basal and usually numerous. They vary in length from 1 to 4 inches. The cauline leaves are also short, and only three or four in number. None of the leaves usually exceeds 4-5 mm. in width. They roll tightly during drought. An osmotic pressure of 12.5-17.9 A. has been determined for their cell sap, and in drier grassland types, 24.2 A.

The foliage has a general level of only about two-thirds that of the flower stalks which are 20-30 inches tall. Two types of plants occur: the usual type is green and scarcely pubescent, but in the other one the leaf sheaths are very downy pubescent and leaden in color. Like *Stipa*, the flower stalks of this grass stand conspicuously above most of the surrounding vegetation so that its abundance is likely to be overrated.

The densely flowered, contracted, spikelike panicles are 2-5 inches long. Blossoming begins late in May, and the height of anthesis

is reached by the middle of June. By late June or the middle of July, depending upon the season, seeds ripen and the flower stalks and cauline leaves are dry. But even in early autumn the dry tufts of dead stems are conspicuous against the background of browns and



FIG. 21.—Fine clump of *Sporobolus heterolepis* in full bloom; flower stalks about 3 feet high.

greens of the autumnal landscape, although about one-third of the basal leaves are still green.

Koeleria is an excellent forage grass and is relished by all kinds of stock.

SPOROBOLUS HETEROLEPIS

Sporobolus heterolepis, prairie dropseed, is distinctly a bunch-forming grass (fig. 21). It was not found in many areas of the prairie,

notwithstanding its wide distribution. It is always most abundant on the driest uplands, where it may dominate local areas, forming 80 or more per cent of the vegetational cover. More usually it occurs as scattered bunches, intermingling with *Stipa spartea* and *Andropogon scoparius*, where it may constitute from 1 to 20 per cent of the cover. From the hilltops and dry upper slopes it sometimes migrates downward, and large, isolated clumps with unusually developed foliage may occur in areas dominated by *Andropogon furcatus*.

The bunches are usually 4-7 inches in diameter but larger ones up to 18 inches occur. They deteriorate as a result of the death of the central part and often break up into numerous tufts which give the appearance of a loose, open, discontinuous sod. In vigorous bunches, under the higher rainfall of the region, the stems are densely aggregated, as many as 100-200 occurring in a single sq. dm. But under less favorable water content of soil the bunches are only 50-75 per cent filled and the number of stems proportionately reduced. Even then the grass is so dense that other species cannot invade.

An examination of the underground parts indicates that the whole bunch may arise from a single plant. It has many short, woody rhizomes 2-3 mm. thick which occur just beneath the soil surface and give rise to dense clusters of roots. The latter are 1-2 mm. in diameter, very abundant, and somewhat intermediate between those of *Stipa spartea* and *Andropogon scoparius*. As the old roots deteriorate, new ones are produced annually, even in the center of the clump. Branches are very abundant, the whole forming a dense network in the soil. The great clusters of stems with swollen bases, the abundant scales and leaf sheaths, and the inch or more of debris collected in the bases of the bunches are all characteristic.

This species renews growth early and develops rapidly. The foliage reaches a height of 8-15 inches by the first of June. In late summer it varies from 8 to 12 inches in height in very thin soil to 15-18 inches under a better upland water supply. In the lowland the foliage is frequently 2 feet tall or more. The stems are characterized by a distinctly enlarged base. These are tough and hard to cut, hence locally this species is known as "wire grass." By midsummer

each stem has about four green leaves, the basal ones having died. The leaves are 18–42 inches long, attenuated and dry near their tips. They have a breadth of only 2–3 mm. and fold tightly during drought. An osmotic pressure of 9.9 A. was determined in June, but this increased to 28.1 A. during the drought in August. The leaves do not stand erect but curve over gracefully, so that the top of the bunch greatly exceeds the basal area, usually measuring about three times as much. Thus the spreading leaves obscure the bare places between the bunches and the sodlike smaller tufts. Hence in areas of nearly pure *Sporobolus*, where the apparent cover is 80–90 per cent, quadrating shows that the basal area is actually about 10 per cent.

Flower stalks begin to appear about July 1, but anthesis usually reaches its height in late August or September. During years of extreme drought few flower stalks are produced, except about the mounds of gophers or other bare areas where the water content is somewhat increased. Under close competition they may scarcely exceed the leaves in height, but usually they stand well above them. Sometimes the broadly spreading panicles reach a height of 3 feet. They are open and loose and 3–10 inches long. The rather large seeds ripen in September and soon fall to the ground. The shining, light green color and the attenuated leaves with dead tips enable one easily to distinguish the species from *Andropogon scoparius*, which perhaps it most nearly resembles.

This dropseed is palatable to all kinds of stock and furnishes considerable forage when it is not allowed to mature.

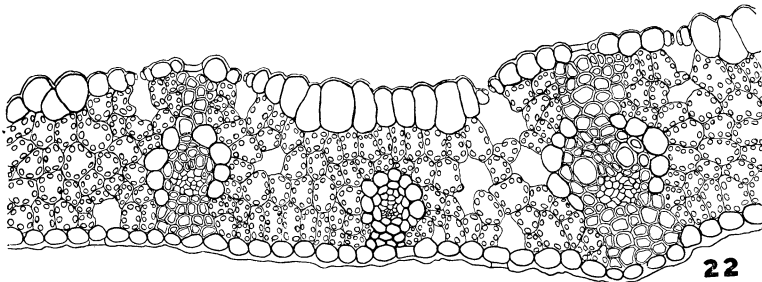
Comparison of leaf structure

It has already been stated that the length and width of the leaves of the grasses vary greatly. Those of the coarse, lowland species such as *Andropogon furcatus*, *Sorghastrum nutans*, and *Panicum virgatum* are often 2 feet in length and 8–18 mm. wide; consequently the leaf expanse is very large. Upland species have much narrower leaves (usually only 2–5 mm. wide); and as in the case of *Andropogon scoparius*, *Koeleria cristata*, etc., they are relatively short. In some species, however, they are of considerable length (sometimes exceeding 3 feet in *Stipa* and *Sporobolus*), but then they are usually much

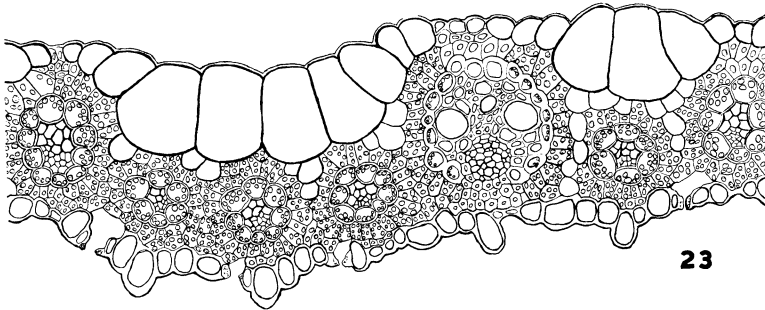
attenuated and often dried at the distal end, so that the area of the individual leaf is comparatively small. It is now our purpose to describe the appearance of the leaves in cross-section, not at length nor in great anatomical detail, but merely to point out several leaf types or patterns and some of the outstanding features of each.

A grass leaf (figs. 22–30) consists essentially of a series of parallel bundles, varying chiefly in size and amount of mechanical and conducting tissue, between which chlorenchyma is supported. Immediately surrounding the bundle is a sheath of cells, often with much thickened, lignified walls. An abundance of mechanical tissue surrounding the vascular bundles protects the water-conducting system from deformation during high winds. Commonly there occurs a second layer of thin-walled parenchyma cells either with or without chlorophyll. Strands of sclerenchymatous tissue ordinarily accompany the bundles and frequently form with the larger ones **I** or **T** beams of mechanical tissue extending across the leaf. The epidermis, especially the lower or dorsal one, is highly cutinized. Over the vascular bundles the epidermal cells are often smaller and thick-walled; while bulliform or motor cells, usually greatly enlarged, occur between the veins. Frequently they lie at the bottom of well defined grooves or occupy the entire thickness of the leaf. They are thin-walled; and when they lose their turgidity through desiccation, the leaf rolls or folds upward or inward. Thus the stomata, which usually occur in rows and ordinarily most abundantly if not entirely in the depressions of the ventral surface, are well protected from water loss. Mechanical tissue is very effective in preventing collapse of the leaf even during wilting and in permitting it to roll. Together with the thick cuticle, it resists excessive bending and twisting before the wind which would result in expulsion of the moist air from the intercellular spaces. The remainder of the leaf is given over to chlorenchyma, except in cases where water-storage tissue occurs.

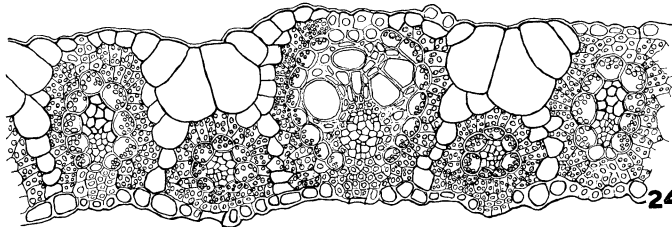
A comparison of figures 22–30 shows that there are among these dominant grasses three general leaf patterns or types. The first (figs. 22–25) is the *Andropogon* or bluestem type. In this type, *Elymus canadensis* shows the smallest amount of mechanical tissue and the least compactness of the chlorenchyma, as well as the smallest bulliform cells. *Andropogon furcatus* has much larger bulliform



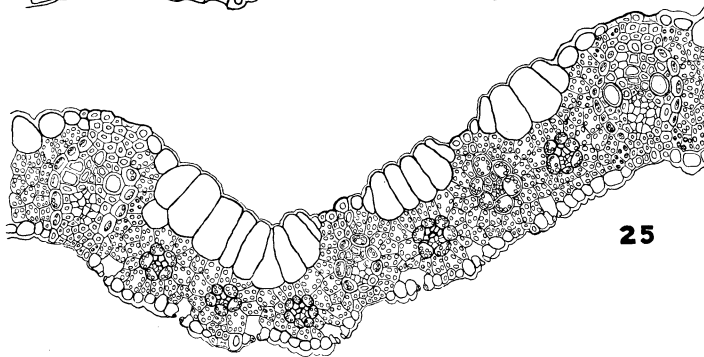
22



23



24



25

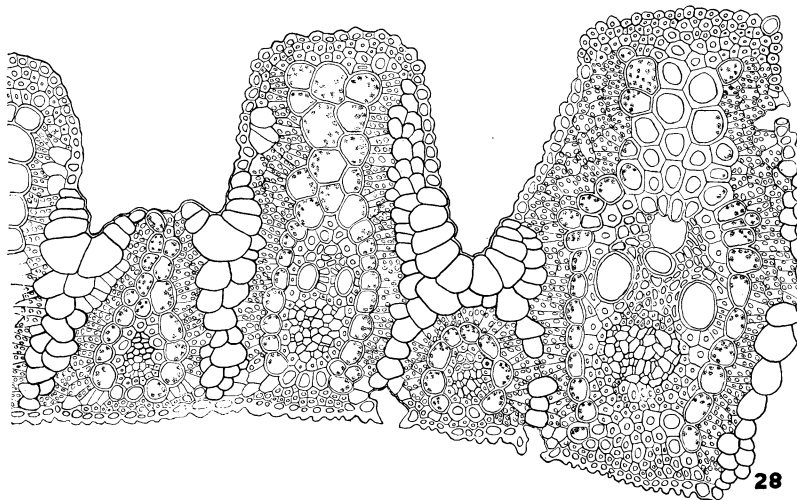
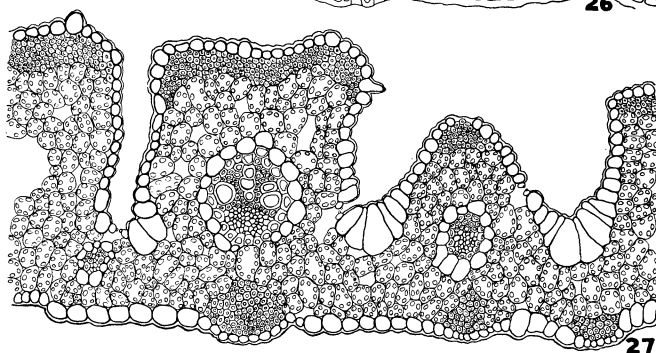
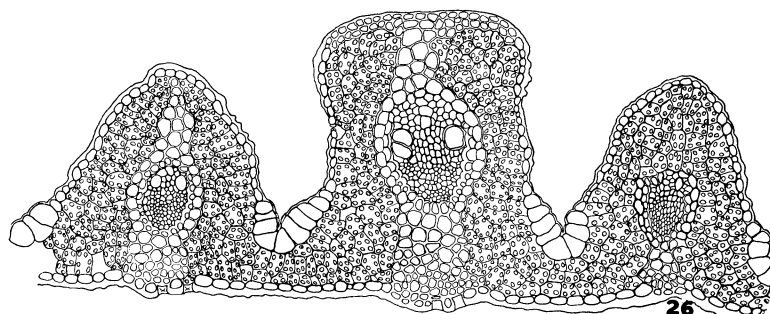
FIGS. 22-25.—Fig. 22, cross-section of leaf of *Elymus canadensis*; fig. 23, cross-section of leaf of *Andropogon furcatus*; fig. 24, cross-section of leaf of *Sorghastrum nutans*; fig. 25, cross-section of leaf of *A. scoparius*; $\times 150$.

cells and more bundles per unit area with a corresponding increase in sclerenchyma. *Sorghastrum nutans* is very similar to *A. furcatus* except that the rows of bulliform cells (as seen in cross-section) are shorter. The leaf of *A. scoparius* is of the same general pattern as the preceding. This narrow leaf folds tightly while the others roll during drought.

Stipa spartea, *Koeleria cristata*, and *Spartina michauxiana* are of the familiar wheat-grass type (figs. 26–28). The leaf is divided into parallel compartments connected by only a few cells of green tissue, with the rolling device prominent in the valleys and the **I** and **T** beams well developed. All have a well developed cuticle. In *Koeleria* and *Spartina* especially, water loss is further retarded by layers of hypodermal cells. The depressions in *Koeleria* are often narrower than in the other species, but the supporting tissue in the beams is not continuous. Xeric characters of *Spartina* are even more marked than those of the other two grasses. The epidermis is extremely heavy; the bundle sheaths and accompanying sclerenchyma are more extensive in this thicker leaf; there is more tissue for water storage; and the compartments of chlorenchyma are almost or entirely separated. Indeed the leaf structure is puzzling, considering the usual habitat, until it is recalled that these very long, broad leaves need much mechanical support, and that during dry weather in summer or autumn this rank grass is sometimes subjected to conditions of rather severe drought. Its ability to exist for years as a relict in rather dry soil is due in part to its xeric leaf structure.

The transition from the wheat-grass type to the beaded or grama-grass type occurs in *Distichlis spicata*. This is similar to *Spartina* except that the smaller leaf compartments below the bulliform cells and between the larger leaf divisions are not present, the whole space being occupied by water-storage cells. These effectually segregate the several distinct chlorophyll-bearing compartments of the leaf (figs. 29, 30). The continuity of the water storage sheath about the largest bundles is interrupted by the presence of an abundance of mechanical tissue. The leaf pattern of *Sporobolus heterolepis* is also of the grama-grass type.

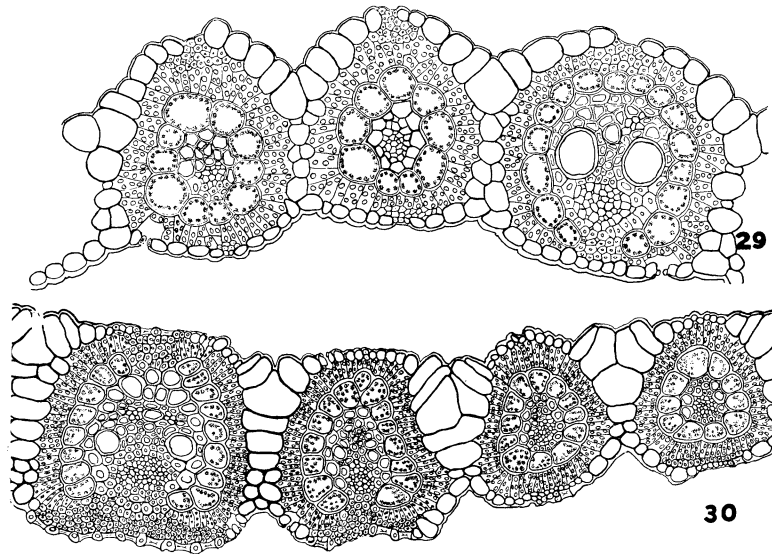
A comparison of figs. 22–30 shows that there is a progressive decrease in the proportion of the leaf used for photosynthesis from the bluestem to the grama-grass type. In *Elymus*, for example, the



FIGS. 26-28.—Fig. 26, cross-section of leaf of *Stipa spartea*; fig. 27, cross-section of leaf of *Koeleria cristata*; fig. 28, cross-section of leaf of *Spartina michauxiana*; $\times 150$.

chlorophyll-bearing tissue is approximately 55 per cent of the cross-sectional area; in *Stipa* it is 51 per cent; but in *Bouteloua racemosa* it falls to only 44 per cent.

All of the leaves exhibit morphological structures characteristic of grasses of arid climates although in some these are less marked than in others. The leaves of even the least xeric, as regards water



FIGS. 29, 30.—Fig. 29, cross-section of leaf of *Panicum virgatum*; fig. 30, cross-section of leaf of *Bouteloua racemosa*; $\times 150$.

content of soil, are regularly subjected to dry, hot winds during certain periods. The leaves of *Andropogon scoparius* and *Sporobolus* fold tightly during drought; all of the other leaves roll.

Summary

1. A study of the tall-grass prairie from southern South Dakota to northern Kansas and eastward into Iowa reveals several patterns or types of vegetation. The big bluestem type is the most extensive and the most important of those found on the lowlands. It is characterized by the single species, *Andropogon furcatus*, which alone often constitutes 80 or more per cent of the vegetation. *Sorghastrum nutans* is a close ecological equivalent which associates with it, but it is in general much less important.

2. *Spartina michauxiana* covers extensive areas of wet, poorly aerated soil with tall, dense, and often nearly pure stands. *Panicum virgatum* and *Elymus canadensis* form an intermediate lowland type of much less extent than either of the preceding.

3. *Andropogon scoparius* constitutes the most extensive upland type and easily exceeds in importance all other upland species combined. *Stipa spartea* is the dominant of another upland type found on steep slopes and ridges in the central and especially the northern part of the area. *Sporobolus heterolepis* exhibits a minor, dry upland pattern. *Bouteloua racemosa* is a minor constituent of all the grassland types, except *Spartina*, occurring less abundantly in the most xeric ones. *Koeleria cristata* is intermixed with *A. scoparius*, *S. spartea*, and *S. heterolepis*, thus showing a preference for dry uplands.

4. The lowland species, except *Elymus* and *Bouteloua*, are sod formers; those of the upland are bunch formers, although *Andropogon scoparius* regularly forms sod-mats under favorable conditions. *Elymus* and *Bouteloua* form either bunches or a poorly developed sod.

5. The chief "weapons" of competition of the tall, lowland dominants are their ability to endure shade and the rapid development of rhizomes resulting in the formation of a dense sod. Upland species rely upon successful competition for water and ability to withstand drought.

6. The seedlings of all species develop rapidly, tiller freely, and under favorable conditions without competition may produce seed the first summer, although under natural conditions two and often three years are required.

7. Root depths of 1.5-3 feet are attained the first season by various lowland species and 1-1.5 feet by those characteristic of upland. Mature root systems of lowland species are likewise in general deeper (4-10 feet) than those of the drier upland soil (1.5-5.5 feet). Those of lowland are much coarser and usually penetrate more vertically downward, however, while those of upland are fine, profusely branched, and widely spread.

8. *Stipa* and *Koeleria* begin growth in March, blossom in late May or June, and make a renewed growth in autumn. *Elymus* likewise starts growth in March; the other species about the middle of April.

Anthesis begins in late July and reaches its height in August or early September.

9. Three general types of leaf structure are evident: the bluestem type, including *Elymus*; the wheat-grass type exhibited by *Stipa*, *Koeleria*, and *Spartina*; and the grama-grass type as shown by *Bouteloua*, *Panicum*, and *Sporobolus*. All show pronounced xeric structures.

10. Osmotic pressures in the various grasses varied from 7.5 to 14 A. during the spring and early summer when the water supply was abundant and growth vigorous. No consistent differences between upland and lowland species were found, but during a severe summer drought the more xeric species showed about twice the osmotic pressure of those of lowlands. These ranged from 22.4 A. for *Stipa*, 24.2 A. for *Koeleria*, and 28.1 A. for *Sporobolus* to 30.4 A. for *Andropogon scoparius*. *Panicum* gave a pressure of 13.7 A. and *Andropogon furcatus* of only 14.5 A. Other lowland species gave somewhat similar results, relict *Spartina* reaching a maximum of 16.4 A. Thus there seems to be a clear relationship between water content of soil and osmotic pressure of the cell sap, species of the drier soils developing the higher osmotic pressures.

11. All of the dominant grasses have excellent forage value, especially if they are grazed or cut for hay before the coarse flower stalks of the late-blooming species become hard and fibrous.

UNIVERSITY OF NEBRASKA
LINCOLN, NEB.

[Accepted for publication October 2, 1931]

LITERATURE CITED

1. CLEMENTS, F. E., and WEAVER, J. E., Experimental vegetation. Carnegie Inst. Washington. Publ. no. 355. 1924.
2. CLEMENTS, F. E., WEAVER, J. E., and HANSON, H. C., Plant competition. Carnegie Inst. Washington. Publ. no. 398. 1929.
3. WALTER, HEINRICH, Die Hydratur der Pflanze. pp. 68-69. 1931.
4. WEAVER, J. E., The ecological relations of roots. Carnegie Inst. Washington. Publ. no. 286. 1919.
5. ———, Root development in the grassland formation. Carnegie Inst. Washington. Publ. no. 292. 1920.
6. WEAVER, J. E., and HIMMEL, W. J., The environment of the prairie. Cons. and Surv. Div. Univ. Nebr., Bull. 5. 1931.