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RELATIVE DROUGHT RESISTANCE OF SEEDLINGS OF DOMINANT PRAIRIE GRASSES

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Recent study of the severe damage to native midwestern grasslands resulting from the great drought was fundamentally an investigation of drought resistance of the various species of dominant grasses and accompanying forbs (Weaver and Albertson, '39, '40). Studies extending throughout the entire eight- or nine-year period of drought, especially those concerned with recharting permanent plots, have resulted in an accumulation of evidence regarding relative drought resistance of the various species (Albertson and Weaver, '42). Extensive field studies on the role of seedlings in recovery of midwestern ranges from drought have added much information on this subject (Weaver and Mueller, '42). With the aid of Dr. F. W. Albertson, lists of species, arranged in their approximate order of drought resistance as determined by field studies, were made in 1940 for both true and mixed prairie. It was realized that a few species, because of their very early development, were at least partly drought evading (table I). Since the most critical stage in the life of a plant is usually that of the seedling, final experimental evidence of relative drought resistance was sought by growing large numbers of seedlings under the same conditions of soil drought or soil and atmospheric drought.[1]

Table I. *Lists of dominant species of mixed and true prairie arranged in approximate sequence of decreasing resistance to drought as determined by observation and experiment in the field.* The last four species in each column are postclimax tall grasses.

Mixed Prairie	True Prairie
Bouteloua gracilis	*Stipa spartea*
Buchloe dactyloides	*Sporobolus heterolepis*
Sporobolus cryptandrus	*Agropyron smithii*
Agropyron smithii	*Bouteloua curtipendula*
Bouteloua curtipendula	*Sporobolus asper*
Aristida longiseta	*Andropogon scoparius*
Aristida purpurea	*Andropogon furcatus*
Andropogon scoparius	*Panicum virgatum*
Andropogon furcatus	*Sorghastrum nutans*
Panicum virgatum	*Elymus canadensis*
Sorghastrum nutans	
Elymus canadensis	

Experiments on Soil Drought

Seeds of 15 species of prairie grasses were sown in the greenhouse during June, 1941. They were *Agropyron smithii* Rydb., *Andropogon furcatus* Muhl., *A. scoparius* Michx., *Bouteloua curtipendula* (Michx.) Torr., *B. gracilis* (H. B. K.) Lag., *B. hirsuta* Lag., *Buchloe dactyloides* (Nutt.) Engelm., *Elymus canadensis* L., *Koeleria cristata* (L.) Pers., *Panicum virgatum* L., *Sorghastrum nutans* (L.) Nash, *Sporobolus asper* (Michx.) Kunth, *S. cryptandrus* (Torr.) A. Gray, *Stipa comata* Trin. and Rupr., and *S. spartea* Trin. Four square tubs, 18 inches wide at the top, 15 at the bottom and 11 inches deep, were partially filled with air-dry, silt loam soil. Space was allowed for an upper layer of moist soil 3 inches deep in two of these containers and 4 inches in the remainder. The moist soil, with available water content of 19.5 per cent, was pressed into firm contact with the dry soil beneath and leveled off one-fourth inch below the top of the container.

Seeds were sown in hills an inch apart. Several seeds were placed in a hill and plants were thinned to one per hill shortly after emergence. Species were arranged so that somewhere a plant of any species was adjacent to one of each of the other

[1] Drought is used to imply a condition of the soil or atmosphere, or of both, that prevents or hinders the plant in obtaining sufficient water for its functions. Soil drought is used to define the condition of lack of water in the soil. Atmospheric drought refers to the desiccation of the plant to the point of injury under conditions of relatively high soil moisture (Miller, '38).

species. A planting board, made from galvanized sheet iron, insured proper spacing. The metal was cut to fit just inside the upper rim of the tub and to lie flat on the surface of the soil. It was ruled into inch squares and holes were drilled at each intersection of the lines. In addition to the outermost or buffer hills, this provided places for 225 plants, 15 of each species. Species were numbered according to time required for emergence of seedlings. The holes of the planting board were labeled with these numbers and toothpicks with corresponding numbers were inserted vertically into the soil through the holes. Seeds were sown where indicated by the toothpicks after the board was removed. Buffer rows were sown to blue grama grass (*Bouteloua gracilis*). In two containers, one with 3 inches and the other with 4 inches of moist soil, the seeds were all sown on the same day. Hence, the time of emergence varied with the species. But seeds were sown in the duplicate set of containers on several successive days so that emergence was more nearly simultaneous. Containers will be considered hereafter as experimental plots.

The soil was covered with heavy paper during the period of germination, thus reducing water loss from the surface. The cover was removed as soon as seedlings began to appear. Thereafter, daily applications of water, amounting to 230 cc. per container, were evenly distributed over the surface of the soil in a fine spray. This quantity of moisture merely replaced that lost from the surface soil by evaporation and did not penetrate far into the layer of moist soil. Ventilators in the roof of the greenhouse were closed and a tent was raised over the plants at night and whenever there were rains so that no water, except that purposely applied, reached the plants. Unnatural heating and drying at the sides of the containers were prevented by building a wooden frame around them and packing crumpled newspapers between them and the frame.

Watering was discontinued when seedlings, which were approximately 3 weeks old, had developed from 3 to 5 leaves and attained a height of 3 to 12 cm. The short grasses (*Bouteloua gracilis, B. hirsuta,* and *Buchloe dactyloides*) were beginning to tiller. Water was withheld from plants in plots 1 (4 inches of moist soil) and 3 (3 inches of moist soil) for 15 and 18 days, respectively. Plants in plots 2 (4 inches of moist soil) and 4 (3 inches of moist soil) were watered after 17 days of drought. These periods were long enough to bring about permanent wilting and to dry the tops until many leaves felt brittle. Plants in plot 2 were subjected to a second period without watering lasting 13 days. The numbers and kinds of missing hills were recorded for each plot at the initiation of drought. The first rolling or folding of leaves, the time of their failure to recover during the night, and changes in color were noted. The plants were then watered. Checking of surviving plants was delayed several days after watering to allow growth of any viable buds. Percentage survival for each species was computed by dividing the number surviving at the end of the drought by the number living at its onset. Plants in the buffer rows were excluded from the computations.

Environment within the greenhouse at the University of Nebraska approximated that which seedlings experience out of doors. Large panels of glass across one end of the greenhouse were replaced with woven wire. This opening together with the usual ventilators provided good circulation of air. The average daily maximum and minimum temperatures from July 1 to August 4, as recorded by a hygrothermograph, were 97° and 70° F., respectively. Average day relative humidity was 52, 64, 47, 50, and 51 per cent for 5 weeks from July 1 to August 4, respectively. This was similar to that of open prairie (Weaver and Fitzpatrick, '34). Whitewash, which was applied to the roof of the greenhouse in wide, alternating bands, reduced the amount of light received by the plants on sunny days to 6300 to 5000 foot-candles. These light values, however, were not as low as those often found in the understory of the grasslands during the growing season and were sufficient to produce normal development of stems and leaves when other conditions were favorable.

Results

Seeds of sand dropseed (*Sporobolus cryptandrus*) failed to germinate and only 2 to 4 plants of Indian grass (*Sorghastrum nutans*) and June grass (*Koeleria cristata*) per plot emerged. Good stands were obtained for all other species.

Leaves of plants growing in only 3 inches of moist soil began to roll or fold 4 to 5 days after water was withheld, and turgidity was not regained by any species after 11 days. Evidence of stress appeared in plants growing in 4 inches of moist soil after 6 to 8 days of drought, but 13 days elapsed before all species were permanently wilted.[2] Rolling or folding of leaves began first in blue grama but soon became evident in side-oats grama (*Bouteloua curtipendula*), big bluestem (*Andropogon furcatus*), little bluestem (*A. scoparius*), and tall panic grass (*Panicum virgatum*). Rolling or folding was delayed the longest by hairy grama (*Bouteloua hirsuta*), buffalo grass (*Buchloe dactyloides*), nodding wild rye (*Elymus canadensis*), Indian grass (*Sorghastrum nutans*), and tall dropseed (*Sporobolus asper*). Although western wheat grass (*Agropyron smithii*) occupied an intermediate position with regard to time of rolling or folding of leaves, it was the first of all species to fail to regain turgidity during the night. *Bouteloua hirsuta, Buchloe dactyloides,* and *Elymus canadensis* continued to become turgid when humidity was high 1 to 2 days after other species were permanently wilted.

All plants in plot 1 were wilted before water was applied, some of them feeling dry and brittle between the fingers, but none had bleached to yellow or brown. A higher percentage of the plants in plot 2 felt dry when touched but otherwise conditions were much the same. Symptoms of distress were more evident at the end of the second drought to which this lot was exposed. Drought was still more advanced in plot 3 prior to watering. Plants were wilted and dry, grayish green in color, and some of the older leaves were brown. Greatest distress was shown by plants in plot 4. All were very dry and many were yellow.

Some plants upon receiving moisture soon regained turgidity, others showed no signs of viability for 3 or 4 days, and the remainder failed to survive. Growth in plants with delayed recovery was from terminal buds enclosed by dead sheathing leaves, or from lateral buds which developed into tillers.

Seedlings of dominant prairie grasses were unlike in their ability to endure similar exposures to drought (table II). *Bouteloua gracilis, Buchloe dactyloides,* and *Bouteloua hirsuta* surpassed all others in ability to withstand drying and showed about the same average percentage survival in all plots. It is significant, however, that the survival of *Bouteloua gracilis* was about three times that of either of the other species in plot 4 where drought was most critical. Placing *B. gracilis* first, the order of diminishing ability to endure drought was in the order

TABLE II. *Percentage survival of seedlings of 14 species of prairie grasses after exposure to drought at normal summer temperatures.* Recovery in plot 2 after each of two periods of drought is shown in columns 2*a* and 2*b*, respectively.

Plots →	1	2*a*	2*b*	3	4
Bouteloua gracilis	91	93	93	33	44
Buchloe dactyloides	100	92	92	50	14
Bouteloua hirsuta	92	100	100	27	17
Sporobolus asper	100	100	100	20	0
Bouteloua curtipendula	92	100	73	9	0
Stipa comata	86	80	20	0	0
Andropogon scoparius	93	66	8	0	0
*Sorghastrum nutans**	50	100	0	0	0
Panicum virgatum	87	60	0	0	0
Andropogon furcatus	100	38	0	0	0
Stipa spartea	54	42	0	0	0
Elymus canadensis	46	36	0	0	0
*Koeleria cristata**	25	33	0	0	0
Agropyron smithii	27	0	0	0	0

* Results based on 2 to 4 plants per container.

[2] Permanent wilting is used to indicate lack of recovery under the conditions of the experiment without the addition of water to the soil.

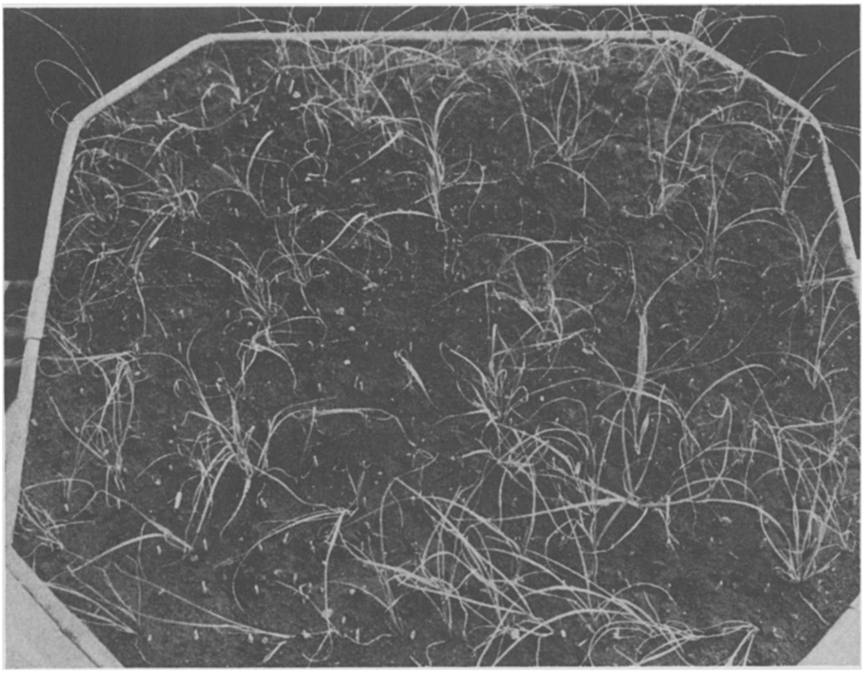

FIG. 1. Container 2, showing survival after a second period of drought of most short grass seedlings (*Bouteloua gracilis, B. hirsuta,* and *Buchloe dactyloides*), all of tall dropseed (*Sporobolus asper*), 73 per cent side-oats grama (*Bouteloua curtipendula*), 20 per cent needle-and-thread (*Stipa comata*), and 8 per cent little bluestem (*Andropogon scoparius*). Other species failed to survive.

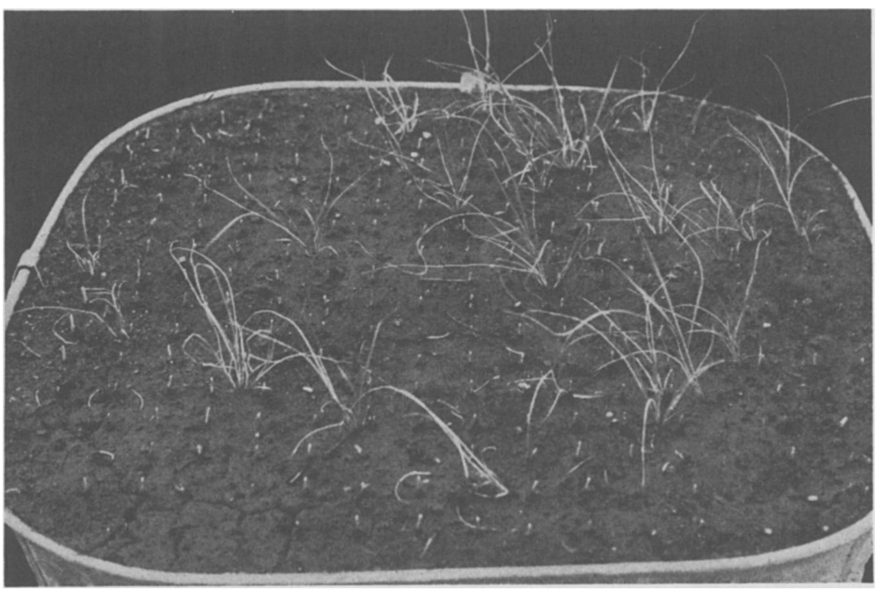

FIG. 2. Container 3 after denudation by drought. Seven buffalo grass seedlings (*Buchloe dactyloides*), 5 blue grama (*Bouteloua gracilis*), 4 hairy grama (*B. hirsuta*), 3 tall dropseed (*Sporobolus asper*), and 1 side-oats grama (*Bouteloua curtipendula*) survived. Toothpicks indicate position of seedlings which failed to survive.

of the arrangement of the species in table II. The positions of *Sorghastrum nutans* and *Koeleria cristata* are somewhat problematical because the number of experimental plants was small. In general, those species which are characteristic of the uplands or which normally occur westward showed greatest drought resistance and those found in the lowlands or in the true prairie, the least.

No species in plot 1 showed a mortality rate of 100 per cent but it was high for *Sorghastrum nutans, Stipa spartea, Koeleria cristata, Elymus canadensis,* and *Agropyron smithii.* No plants of *Agropyron smithii* were alive after the first drought in plot 2 but all other species showed some survival. All plants of *Koeleria cristata, Elymus canadensis, Stipa spartea, Andropogon furcatus, Panicum virgatum,* and *Sorghastrum nutans* were dead after the second drought and only one plant of *Andropogon scoparius* remained alive (fig. 1). Survival in plot 3 was limited to the 3 short grasses, *Sporobolus asper,* and *Bouteloua curtipendula* (fig. 2). The severity of drought in plot 4 was shown by the loss of all but a few short grasses (table II).

Experiments with Hot Wind

Three tubs were filled with soil containing 19.5 per cent available moisture; three others, with soil having only 4.8 per cent. The former are referred to hereafter as mesic plots and the latter, xeric. All were sown according to the same plan used for the experiments on soil drought, and immediately afterwards the top 1 to 2 inches of soil was moistened thoroughly and uniformly. The soil was covered with paper until seedlings began to emerge, and the sides of the containers were insulated as previously described. After the removal of the paper, the soil in each mesic plot received 460 cc. of water daily and that in each xeric one, 230 cc. Environment in the greenhouse was identical with that described for the experiments on soil drought since the containers for both were housed together.

A large galvanized iron container, nearly square in cross-section and 20 inches in diameter, with bottom removed, was placed on its side on a table. Several layers of asbestos were pasted around the outside throughout its length, which was 48 inches, thus providing insulation against loss of heat. Boards fastened across the front end of this tunnel enclosed the bottom 12 inches and left an opening 8 inches wide at the top. A lath frame, 20 inches wide and 22 inches long and covered with clear cellophane which extended downward 8 inches on both sides of the frame, was fastened to the front of the tunnel. Two electric heaters of the round reflector type were removed from their stands and placed in the bottom of the tunnel so that the heat was reflected forward and upward. An electric fan, set back of these, blew the hot air out of the front opening. It was distributed evenly over the plants when the container was set under the cellophane on a small turntable which placed the top of the container at the level of the front opening in the heating tunnel. Grasses growing in the container were thus in light when exposed to heated air but the cellophane together with the shadow from the opaque portion of the tunnel reduced this light to about 1000 foot-candles. Several thicknesses of canvas were hung over the rear of the tunnel, leaving a small opening for ventilation. Temperature was regulated by changing the size of the opening. Readings of air temperature were made at 15 minute intervals. Relative humidity was measured with a cog psychrometer whenever temperature was increased. Wind velocity, which also varied with the size of the opening, ranged from two to six miles per hour. The sides of each container were covered with an asbestos jacket when the plants were subjected to heated air. The turntable was moved one-eighth of a revolution every 15 minutes so that the plants were completely rotated every two hours during the experiment. Treatment of plants varied somewhat for the different containers, hence the procedure and results with each plot are considered separately.

Plants in plot 5 had grown in moist soil for three weeks when treatment with artificial heat was begun. They ranged in height from 5 to 14 cm., depending on the species. *Agropyron smithii, Koeleria cristata, Elymus canadensis,* and *Stipa comata* possessed 2 to 3 leaves per culm and the other species 4 to 5. The short grasses and *Andropogon scoparius* were tillering.

When the plants were first exposed to the hot wind, the temperature was 110° F. and the relative humidity 26 per cent. Treatment at this temperature (110°–113°) was continued 9 hours each day for 6 days. Leaves of most species rolled or folded on the first day and there was some drying of tips but injury did not increase on subsequent days. Leaves of *Bouteloua gracilis, Sporobolus asper,* and *Agropyron smithii* were the first to roll and those of *Bouteloua hirsuta* were the last. All plants were wilted at the end of the sixth day but they had recovered by the following morning. The temperature on the seventh day was kept at 122° for 9 hours. At this temperature relative humidity was reduced to 17 to 15 per cent. Plants soon wilted but none succumbed. The next day temperature was increased to 129° to 135° for 4 hours and to 140° to 153° for another 4 hours. The plants evidenced much wilting and rolling during the first 4 hours and after the final treatment all were wilted and many were dry (fig. 3). No water was added to the soil during the entire treatment but samples of soil taken at the end of the experiment had 13 per cent available moisture. Although the top soil was dry, the young plants had not depleted the deeper soil

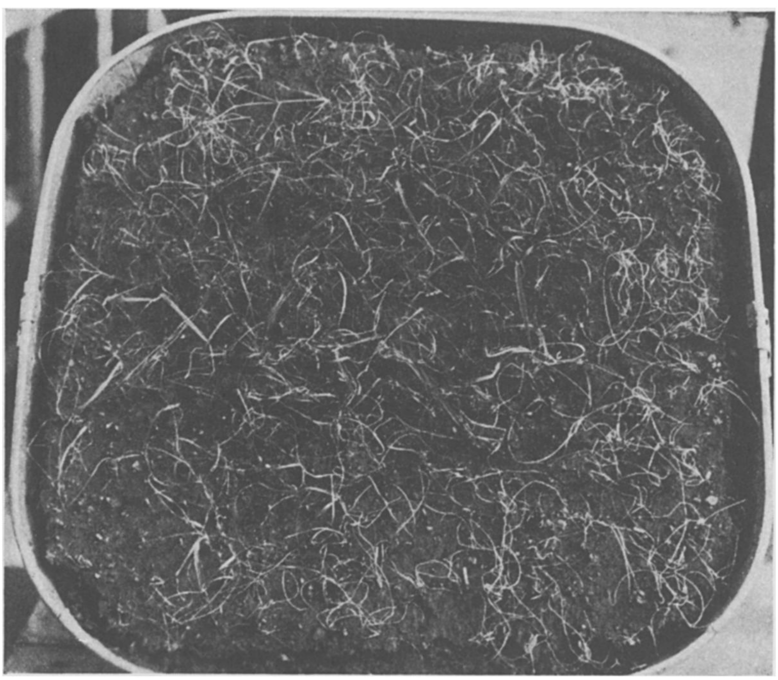

FIG. 3. Seedlings of 12 species of prairie grasses after exposure to day temperatures ranging from 110° to 153° F. for 7 days. All were wilted and many were dry, but western wheat grass (*Agropyron smithii*) and nodding wild rye (*Elymus canadensis*) were the only species with no survival.

TABLE III. *Percentage survival of seedlings of 14 species of prairie grasses after exposure to hot winds for the number of hours indicated at the range of high temperatures shown in the fourth horizontal line*

Plot	5 Mesic		6 Xeric		7 Mesic		8 Xeric		9 Mesic		10 Xeric	
Age (wks.)	3		4		4.5		5		6		6	
Time (hrs.)	4	4	5	1	9	9	9	9	9	9	9	5
Temperature (degrees F.)	129–135°	140–153°	131°	140–145°	129–135°	140°	131–135°	140–145°	129–135°	140°	131°	140–145°
Bouteloua gracilis	100	75	100	100	100	86	100	93	100	100	100	100
Buchloe dactyloides	100	91	100	100	100	93	100	100	100	100	100	100
Bouteloua hirsuta	100	93	100	100	100	100	100	100	100	100	100	100
Sporobolus asper	100	64	100	93	100	85	100	100	100	100	100	100
Bouteloua curtipendula	100	89	100	100	100	100	100	100	100	100	100	91
Stipa comata	100	86	100	33	100	100	100	92	100	100	100	92
Andropogon scoparius	100	86	100	73	100	93	100	100	100	100	100	100
Andropogon furcatus	100	86	100	70	100	100	100	93	100	100	100	100
Panicum virgatum	100	86	100	14	100	100	100	53	100	100	100	93
*Sorghastrum nutans**	100	33	100	75	100	100	—	—	100	100	100	100
Stipa spartea	—	—	—	—	100	91	100	75	—	—	—	—
*Koeleria cristata**	—	—	—	—	100	100	100	0	100	100	100	100
Elymus canadensis	100	0	100	0	100	55	100	0	100	60	100	0
Agropyron smithii	100	0	100	0	100	46	100	0	100	93	100	0

* Based on 2 to 4 plants per container.

of its moisture. Many plants were injured at temperatures of 110° to 135° but none fatally. There were deaths among all species when the temperature became as high as 153°, and no *Elymus canadensis* or *Agropyron smithii* survived (table III). Such a temperature was fatal, however, to but a small percentage of *Bouteloua curtipendula, B. hirsuta,* and *Buchloe dactyloides.*

When the plants in plot 6 (xeric) were exposed to hot wind at the age of 4 weeks, most of them were approximately 2 cm. shorter than corresponding mesic plants. Seedlings of *Bouteloua gracilis* were tallest, ranging in height from 8 to 12 cm. *Buchloe dactyloides* and *Bouteloua* spp. were tillering, the number of tillers per plant ranging from 1 to 3. The color of the plants was normal but leaves of *Bouteloua gracilis* had been rolling. Soil samples indicated that available soil moisture was nearly exhausted.

The initial temperature of the hot wind was 110° F. and relative humidity 25 per cent. Temperature was increased to 122° after 4 hours and maintained at that point for 4 hours. The leaves of all plants rolled or folded but there was no permanent injury since all were turgid and had normal color the following morning. The second day, the plants were subjected to a temperature of 131° and a relative humidity of 15 per cent for 5 hours. All leaves again rolled or folded under the great stress of evaporation. The temperature was increased to 140° to 145° for 1 hour after which it was reduced to 130° for 4 hours. Considerable leaf-tip injury and the death of all *Elymus canadensis, Agropyron smithii,* and much of *Panicum virgatum* and *Stipa comata* were evident the following morning. A temperature of 131°, accompanied by relative humidity of 15 to 16 per cent was maintained for 2 days (9 hours each) thereafter with little further injury. The final check revealed 100 per cent survival of *Buchloe dactyloides* and the three species of *Bouteloua.* Only 1 plant of *Sporobolus asper* was dead and about one-fourth of the plants of the Andropogons (table III).

Plants in the moist soil of plot 7 had

attained an age of 4.5 weeks when the experiment was begun. Except for *Koeleria* which was only 1 to 1.5 cm. tall, heights of 8 to 35 cm. had been attained, *Bouteloua curtipendula* overtopping all other species. *Agropyron smithii, Stipa spartea, Koeleria cristata, Elymus canadensis, Andropogon furcatus,* and *Stipa comata* had failed to tiller but other species had developed additional culms and *Buchloe dactyloides* possessed as many as 13. Species lacking tillers, except *Andropogon furcatus,* had developed only 2 to 3 leaves per culm, but species with tillers and *A. furcatus* had 4 to 7 leaves per stem.

As before, the temperature was 110° F. when plants were first placed in heated air. After 4 hours the temperature was increased to 120° for another 4 hours. Relative humidity during these periods ranged from 29 to 22 per cent. No rolling or folding of leaves and no injury to tops occurred. The soil was watered thoroughly at the end of the day. The following day, temperatures were kept between 129° and 135° for 9 hours, and these were accompanied by relative humidity of about 15 per cent. Late in the afternoon, the plants were somewhat wilted but there was no permanent injury since all were turgid the following morning (fig. 4). On the last day, temperature was maintained at 140° for 9 hours. A high rate of evaporation accompanying the high temperature and low humidity (13 per cent) dried the leaves, but stems of certain species remained turgid. The plants were watered at the conclusion of the experiment. About half of the seedlings of *Agropyron smithii* and *Elymus canadensis* survived exposure to a temperature of 140° when soil moisture was plentiful (table III). Other species did not suffer serious losses and survival was complete for *Bouteloua curtipendula, B. hirsuta, Stipa comata, Andropogon furcatus, Panicum virgatum, Sorghastrum nutans,* and *Koeleria cristata.*

Plants in plot 8 were 5 weeks old when subjected to high temperatures. Seedlings of *Bouteloua gracilis,* which had grown in this xeric plot, were much the same height (about 13 cm.) as mesic seedlings of the same age, but other spe-

FIG. 4. Seedlings in mesic plot still vigorous and erect after 9 hours exposure to 129° to 135° F. Only rarely was a leaf tip dried.

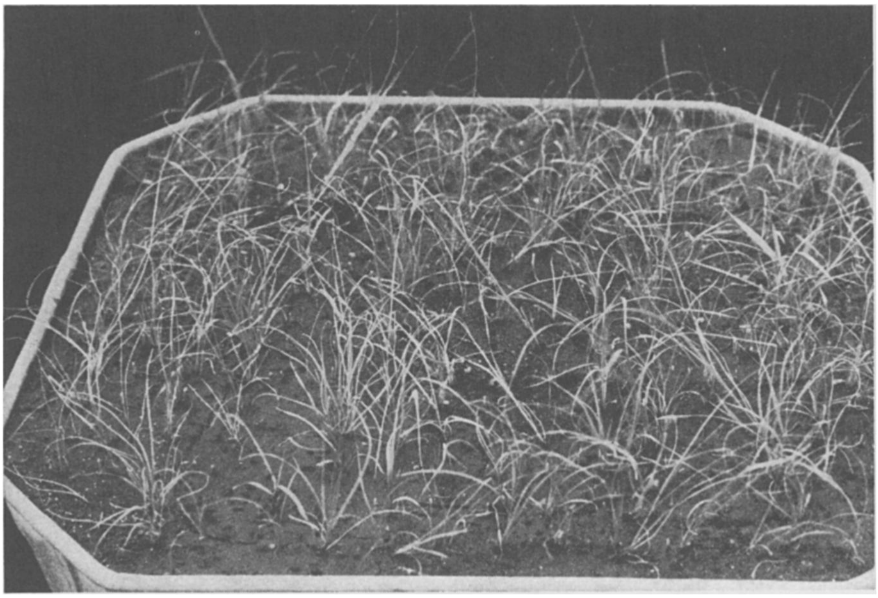

FIG. 5. Xeric plot showing but slight damage to seedlings of buffalo grass (*Buchloe dactyloides*) and the three gramas (*Bouteloua gracilis, B. hirsuta,* and *B. curtipendula*) after 9 hours at 140° to 145° F. Other species had succumbed or showed injury of leaves.

cies were only about half as tall (5 to 11 cm.) as corresponding mesic plants. The Andropogons, *Sporobolus asper,* and *Buchloe dactyloides* possessed 1 to 2 fewer leaves in xeric than in mesic conditions but among other species the number of leaves was about the same in both environments. Tillering was reduced about one-half. *Andropogon scoparius,* and the three Boutelouas had developed 1 to 3 tillers and *Buchloe dactyloides,* 6 to 8. Many of the seedlings, especially *Bouteloua gracilis,* had earlier given evidence of a limited supply of moisture by rolling or folding of leaves during the day. Color of leaves, however, was normal.

The usual daily allotment of water (230 cc.) was sprinkled on the soil before the experiment began. The amount of available moisture in the soil was 1.9 per cent. The initial temperature of 110° was gradually increased to 122° during the forenoon and held at that point until 5 p.m. Relative humidity was 41 per cent one hour after treatment was begun and 21 per cent four hours later. Protective mechanisms in the leaves became active immediately after the plants were placed in the tunnel and after one hour all were rolled or folded except *Panicum virgatum,* which delayed folding for nearly three hours. All plants regained turgidity during cessation of treatment in the night. The following day temperature was increased to 131° to 135° for 9 hours and this was accompanied by a relative humidity of only 15 per cent. Again leaves on all plants quickly rolled or folded and at the end of the day those of *Elymus canadensis* and *Agropyron smithii* were injured somewhat. Recovery during the night was complete except for the injured leaves. Late in the afternoon, after another 9 hours at temperatures of 140° to 145° and relative humidity of 12 per cent, all seedlings except *Buchloe dactyloides* and *Bouteloua hirsuta* appeared dry. The next morning, however, *B. gracilis, B. curtipendula,* and many plants of *Andropogon scoparius,* as well as *Buchloe dactyloides* and *Bouteloua hirsuta* showed little injury (fig. 5). Survival was high for all species except *Panicum virgatum, Stipa spartea, Koeleria cristata, Elymus canadensis,* and *Agropyron smithii,* which lost 47, 25, 100, 100, and 100 per cent, respectively (table III).

Plants in plot 9 had been growing under mesic conditions for nearly 6 weeks when they were transferred to the wind tunnel. *Koeleria cristata* and *Stipa comata* were both short, with average heights of 1.5 and 6.5 cm., respectively. All other species had average heights of 11 to 24 cm. All species except *Agropyron smithii, Koeleria cristata, Andropogon furcatus,* and *Stipa comata* were tillering. *Buchloe dactyloides* possessed as many as 10 to 13 tillers; *Bouteloua hirsuta,* 3 to 8; *B. curtipendula,* 4; and *B. gracilis,* 2 to 4. *Agropyron smithii, Elymus canadensis, Koeleria cristata,* and *Stipa comata* had developed only 2 to 3 leaves per culm but all other species had 4 or more.

The initial temperature of 110° F. to which these plants were exposed was gradually increased until it reached 125° at the end of 5 hours. It was held at this point for 4 hours. Relative humidity decreased from 31 to about 20 per cent during the same period. The leaves did not roll or fold and there was no leaf-tip injury. The soil was watered at the end of the day and hot wind discontinued during the night. Temperature the following day was kept between 129° and 135° and relative humidity was about 17 per cent. After 9 hours, the plants still showed little injury. Some leaves of *Bouteloua gracilis* were rolling and other plants were somewhat wilted. Injury to tips of leaves was rare. The following day, the plants were under great stress of evaporation when they were subjected to a temperature of 140° and relative humidity of 10 per cent for 9 hours. Although a wind as hot as 140° was injurious to the tops of all species, it was fatal to only *Elymus canadensis* and *Agropyron smithii.* Even among these, survival was high with 60 to 93 per cent, respectively (table III). Samples of soil taken at the end of the treatment showed 5.1 per cent moisture still available for growth.

Plants in plot 10 had grown for 6 weeks under xeric conditions. They ranged in height from 1.5 cm. (*Koeleria cristata*) to 12 cm. (*Bouteloua curtipendula*). *Stipa comata, Elymus canadensis, Koeleria cristata,* and *Agropyron smithii* had developed 2 leaves each; all other species had 4. *Buchloe dactyloides* and 3 species of *Bouteloua* were tillering. All species had rolled or folded their leaves during the day for some time previous to the experimental treatment. Leaves of *Andropogon scoparius* were folded and those of *Bouteloua gracilis* were rolled the morning the plants were placed in the tunnel. The grayish green color of the foliage further indicated the xeric environment. The soil contained about one per cent available moisture.

After 5 hours at 110 F., temperature was increased to 122° for 4 hours. The relative humidity which accompanied this high temperature was 20 per cent. After a night of recovery, the plants showed no injury other than the usual rolling or folding. That day a temperature of 131° was accompanied by a relative humidity of 15 per cent. The leaves rolled or folded during 9 hours in this environment, but the plants suffered no permanent injury. Next day, *Agropyron smithii* and *Elymus canadensis* succumbed after exposure to 140° to 145° for 5 hours but other species showed only minor losses or none (table III).

Discussion

A good agreement exists between resistance of various species to experimental soil and atmospheric drought and to natural drought as determined by studies in the field. Aamodt ('35) found that varieties of wheat which were known to be drought-resistant under field conditions were less severely injured under artificial tests than varieties known to be non-drought resistant. Hunter, Laude, and Brunson ('36), in experiments on the effects of heat and drought on inbred lines of maize, used temperatures of approximately 140° F. and a relative humidity of 30 per cent. The various tests gave consistent results and agreed well with field trials. Shirley and Meuli ('39) obtained results from laboratory machine tests on drought resistance and on field survival of conifers during extremely dry periods which were in good agreement. Schultz and Hayes ('38), working with hay and pasture grasses and legumes, found very good agreement between the results of artificial drought and those obtained under field conditions.

Temperatures to which seedling grasses were exposed were similar to those to which seedlings growing on the drought-stricken prairies and ranges experienced on hot summer afternoons. Average daily maximum air temperatures per week of 111° F., 5–7 inches above the soil, have been recorded at Lincoln. Air temperatures of 124° to 140° were not uncommon just above the bared soil during drought, and readings of 136° to 153° have been recorded in the surface of the dry black chernozem and prairie soils. *Agropyron smithii* and *Elymus canadensis,* both of which demonstrated inability to survive temperatures greater than 140°, often escape such extreme heat by emerging early in spring and becoming established before summer. Seedlings of Elymus appear late in March or early in April and have been known to fruit by the end of June (Mueller, '41). A temperature of 140° to 145° F. was not a serious limiting factor to seedlings of other species except *Panicum virgatum* and *Stipa comata* which showed losses as great as 86 and 67 per cent, respectively.

There was no loss of plants and only slight injury to leaves at temperatures below 135° when soil moisture was available. This was true in both moist and dry soil. Seedlings of all species died at lower temperatures when soil moisture was exhausted for a sufficient time. This would indicate that injury to dominant prairie grasses by hot wind occurs only when soil moisture is depleted to a point where the plant cannot absorb water rapidly enough to replace that lost by transpiration. The exact nature of damage at temperatures above 140° is not known. It is possible that the heat may have injured directly by coagulation of the protoplasm, but it is probable that high temperature indirectly caused death by promoting excessive water loss which resulted in dehydration of the protoplasm or in mechanical destructive disturbances resulting from dehydration of the cells (Iljin, '30). The roots of seedlings of *Agropyron smithii,* a species of northern extraction, to which a temperature of 140° to 145° was always fatal, are only sparingly branched (Weaver and Mueller, '42) and are poorly equipped to offset a high rate of transpiration. The vigorous roots of short-grass seedlings, on the other hand, early develop extensive absorbing surfaces and are well suited to supply large quantities of moisture to the tops. These grasses were least injured at high temperatures. Aamodt and Johnston ('36) found that capacity of developing root systems rapidly in the early stages of growth was an important factor in drought resistance in wheat.

The order of resistance of seedlings to drought—*Bouteloua gracilis, Buchloe dactyloides, Bouteloua hirsuta, Sporobolus asper, Bouteloua curtipendula, Stipa comata, Andropogon scoparius, A. furcatus, Panicum virgatum, Sorghastrum nutans, Stipa spartea, Koeleria cristata, Elymus canadensis,* and *Agropyron smithii*—is somewhat altered from that given in results on soil drought experiments (table II) by the inclusion of losses sustained in atmospheric drought. The short grasses, however, were most drought resistant under both conditions and western wheat grass the least. This latter arrangement is somewhat more in agreement with observations in the field (table I) especially with regard to the positions of *Andropogon furcatus, Panicum virgatum, Sorghastrum nutans,* and *Elymus canadensis.*

The behavior of seedlings during exposure to hot wind was influenced but little by their age. Percentage survival was somewhat less for certain tall-grass seedlings 3 and 4 weeks old than for those 2 to 3 weeks older, when temperature and previous treatment were the same, but, in general, responses were much the same.

The fact that seedlings of *Bouteloua gracilis* in dry soil were nearly as large as mesic seedlings of the same age while seedlings of other species were much dwarfed is highly significant with respect to their ability to endure drought. Maximov ('31) has pointed out that the ability to continue photosynthesis, long after mesophytes have ceased doing so, is an important advantage possessed by the xerophyte.

Summary

Mixed plantings of seedlings of 14 species of dominant prairie grasses were tested for resistance to drought at ordinary summer temperatures. Only a few plants, all of which were short grasses, survived where drought was most critical. Of these blue grama (*Bouteloua gracilis*) showed the greatest drought resistance, three times as many plants surviving as those of hairy grama (*B. hirsuta*) and buffalo grass (*Buchloe dactyloides*) which were next in order. Western wheat grass (*Agropyron smithii*) was least able to resist drought.

There was no mortality and only slight damage to seedlings subjected to hot winds of 135° F. when soil moisture was available. Leaves of the short-grass seedlings, listed above, were scarcely injured by temperatures as high as 145° F. Neither differences of a few weeks in age nor previous exposure to drought had any significant effect on the survival of seedlings which were exposed to hot winds.

When the results of exposure to soil drought and to atmospheric drought were both taken into account, *Bouteloua gracilis* was the most drought resistant. In order of decreasing drought resistance the species were *Buchloe dactyloides, Bouteloua hirsuta, Sporobolus asper, Bouteloua curtipendula, Stipa comata, Andropogon scoparius, A. furcatus, Panicum virgatum, Sorghastrum nutans, Stipa spartea, Koeleria cristata, Elymus canadensis,* and *Agropyron smithii.* In general, species characteristic of uplands or which normally occur westward in mixed prairie were more resistant, and those in the lowlands or in the true prairie less resistant to drought.

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