DROUGHT RESISTANCE IN RANGE AND PASTURE GRASSES[1]

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(WITH EIGHT FIGURES)

Introduction

Rainfall is the limiting factor in the success of the livestock industry on the western range. Precipitation is especially critical in the southern Great Plains, the Southwest, and the semi-desert areas of the Intermountain Region. Here drought and its accompanying overgrazing constitute the major range problems and have been responsible for serious depletion of the forage resources of the region.

NELSON (**29**) has shown that in years of drought basal area of black grama may fall as low as 10 or 11 per cent. of the maximum stand and 20 per cent. of a 13-year average. CRADDOCK and FORSLING (**8**) found in Southern Idaho that the volume of forage produced varied from 41 above to 33 per cent. below the nine-year average, largely as a result of winter and spring precipitation. Drought and overgrazing together result in much greater reduction than does drought alone or drought and moderate grazing (**46, 47**). STEWART (**43**) reported that Forest Service studies on western Utah winter ranges show that the drought from 1931 to 1934 caused a 20 per cent. decrease in available forage plants on ungrazed plots, but on overgrazed areas, depletion was approximately 60 per cent. SAVAGE (**36**) and SAVAGE and JACOBSON (**37**), studying drought injury in the central and southern Great Plains, reported that as grazing was intensified all grasses decreased in all areas where drought was severe. LANTOW and FLORY (**17**), working on semi-desert grassland of New Mexico, concluded that permanent injury may be caused by drought on overgrazed range, but that on properly grazed range the recovery of the grass stand with increased precipitation is rapid. U. S. Forest Service workers (**6, 7, 29, 33**) have continuously stressed the injurious effect of drought on range plants. BOUGHMAN (**3**) showed that the root growth of several different range grasses is inhibited by clipping, the degree varying directly with the amount of clipping. SILKER (**41**) found that drought survival of western wheat grass seedlings depended upon the formation of rhizomes.

Most workers agree that the physiological bases for drought and frost resistance are similar. There is disagreement, however, in the theories of the mechanism of resistance. Several workers (**5, 10, 19, 20, 30, 34**) have emphasized the importance of bound or "unfreezable" water in drought and frost resistance. This idea is questioned by other investigators (**40, 49**). PALTRIDGE and MAIR (**32**) concluded that xerophytes had a high water balance, but later work along this line by BAILEY (**1**) and KLOMP (**16**) failed to show a correlation between water balance and the xerophytic nature of

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the natural habitat of the plants. High concentration of cell sap is often associated with drought resistance. LEBEDINCEV (**18**) stated that the main rôle in determining the water retaining capacity of plant cells was played by osmotic substances and not by colloids. Other workers (**34, 42, 44**) have stressed the importance of hydrophyllic colloids in this rôle.

LOOMIS (**22**) has shown that food reserves are necessary for differentiation processes such as occur in plants during hardening. It is generally agreed (**21, 26, 27, 44**) that carbohydrate reserves are essential to the development of frost resistance in plants. Several investigators in this field (**34, 42, 44**) believe that carbohydrates are also necessary for drought resistance since the hardening process is essentially the same. Other workers (**4, 26, 27, 35, 48**) have shown the relationship between grazing and food reserves. Several workers (**11, 18, 21, 31, 38, 39, 44**) have investigated the changes taking place in plants during the hardening process. MAXIMOV (**24, 25**), in 1929, made a comprehensive review of the basis of frost and drought resistance up to that date. SCARTH, LEVITT, and SIMINOVITCH (**21, 38, 39**) have done considerable detailed research on the nature of cold and drought resistance in plants. They found that hardened protoplasm is less susceptible to coagulation or rupture during drought, is more permeable, has a lower viscosity, is more colloidal, and has a greater water-binding capacity than does unhardened protoplasm.

The emphasis in past work has been on resistance to dehydration with little attention to the independent or interacting effects of temperature. High temperatures normally accompany periods of drought, and, with the removal of the protecting cover by overgrazing, lethal soil temperatures become a threat to the survival of the grass roots and rhizomes. HEILBRONN (**12**), in 1924, and HEILBRUNN (**13**), in 1928, made detailed studies on the effect of high temperatures on living protoplasm. BELEHRADEK (**2**), in 1935, made a very comprehensive review of work done up to that date on temperature and living matter. He pointed out that heat injury is so complex that it cannot be explained by any one theory. He also called attention to the fact that the time factor in heat action is important, a fact which has been overlooked by many workers. SAVAGE (**36, 37**) and MUHLER and WEAVER (**28**) have recognized the damaging effect of high temperatures on range grasses.

Much time has been spent in studies of drought resistance in forage plants, and several attempts have been made to develop a simple and reliable method of testing the ability of these plants to withstand arid conditions. Some progress has been made, but no substitute for field reactions under drought conditions has been developed. Our work has been directed toward the solution of the problems of temperature injury and the use of resistance to high temperature as an index of drought resistance. Our purposes have been: (a) to test the heat resistance of various range grasses as a factor in drought resistance; (b) to determine the effect of carbohydrate supply and protoplasmic differentiation on the ability of plants to withstand heat; and

(c) to investigate the relationship of overgrazing to plant food reserves, soil temperatures, and drought resistance.

Methods

Studies of the effect of clipping and drought on heat resistance

Grasses with natural habitats differing in moisture and temperature conditions were selected for study. The following species were used: (a) Bermuda grass [*Cynodon dactylon* (L.) Pers.] which thrives in the hot climate of the South; (b) buffalo grass [*Buchloe dactyloides* (Nutt.) Engelm.] which has the reputation of being very drought resistant on the Great Plains; (c) bluestem or western wheatgrass (*Agropyron smithii* Rydb.) which has a wide distribution on the western range on arid and semi-arid areas; and (d) slender wheatgrass [*Agropyron pauciflorum* (Schwein.) Hitchc.] which grows chiefly in the foothills and mountains of the western range.

Grasses were transferred from field conditions to greenhouse ground plots where they were subjected to different treatments for a period of two months. Drought conditions were maintained on one series of plots while the other series was kept well watered. Plants on the south half of each plot were clipped bi-weekly to a 2-inch height. This procedure provided the following treatments for each species: (a) watered and clipped; (b) watered and unclipped; (c) dry and clipped; and (d) dry and unclipped. This procedure was used in an attempt to produce plants of four different food reserve levels ranging from very low in the first treatment to very high in the fourth treatment. The plants subjected to drought would presumably be hardened while the well-watered plants would be unhardened. The same treatments were applied to bluegrass in bench flats in the greenhouse. The same soil mixture was used, and flats for the various treatments were located at random.

Following drought and clipping treatments, plant samples were taken from each plot at mechanically spaced intervals and subjected to heat treatment. Individual plants were as uniform in size as possible. The rhizomes or stolons were cut to $1\frac{1}{2}$-inch lengths. Roots were left intact and kept moist between wet paper towels. Lots of eight plants were used for each treatment, and each treatment was run in duplicate. The plants were placed in glass tubes, which were stoppered with cotton-covered cork, and immersed in a constant temperature water bath. Control samples were placed in similar tubes and kept at room temperature. The water bath was held at $48 \pm 0.1°$ C. (a temperature indicated by preliminary tests) and treatments of 0, $\frac{1}{2}$, 1, 2, 4, 8, and 16 hours time were given to each species.

After the heat treatment, the plants were transplanted immediately to an outside bed, watered well, and permitted to grow for a period of approximately four weeks. At the end of this period the recovery of the individual plants in each sample was judged according to a previously arranged rating. Plants of excellent vigor were given a rating of ten, those of moderate vigor six, those of poor vigor two, and the dead ones zero. The standard was based on the control samples, and vigor classes were determined by height, growth, color, and sturdiness. Average ratings were used for the figures.

STUDIES OF FOOD RESERVES OF RANGE GRASSES AS AFFECTED BY GRAZING AND DROUGHT

To ascertain the status of the food supply of range grasses as affected by drought and grazing, and as affecting drought resistance, samples of roots, root crowns, and rhizomes (where present) were collected and analyzed. Plots in near-virgin condition with good stands of wheatgrasses were located on a sagebrush-wheatgrass range near Ogden, Utah. One area was in the undisturbed portion of North Ogden cemetery and another along a railroad right-of-way. One area was covered with a good stand of bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. and Smith] and the other with bluestem. Duplicate ten-gram root samples were taken at each location on June 14 and 15. The plants had reached approximately their maximum vegetative growth, but the moisture supply had been plentiful, and the plants had experienced no drought.

Four representative plots six feet square were selected at each of the two locations. On two of these plots, selected by lot, all vegetation was clipped to a 2-inch height. The plan called for repeated clipping through the summer on these plots, but drought conditions followed the clipping treatment and practically no new growth was made.

On August 28 to 30 of the same summer, duplicate root samples were taken on clipped and unclipped plots. Between samplings only traces of rain had fallen. The average annual precipitation for this area is around eleven inches with most of the moisture falling during the late fall, winter, and early spring. Drought conditions during the period of study were fairly typical. The grass foliage had begun to dry up about two weeks after clipping so they had been subjected to nearly two months of rather severe drought by the time the second root samples were taken. The ten-gram root samples for chemical analyses were obtained by digging twelve plants for each sample; these were taken into the laboratory where the dirt was removed by washing in cold water and the tops were clipped to a ½-inch height. The samples were dried by blotting with paper towels. Roots, rhizomes, and stem bases were included in the samples. The twelve plants from each plot were mixed and ten-gram samples weighed out and immediately placed in jars containing 80 per cent. boiling grain alcohol and steeped for 20 minutes to stop enzymatic action and preserve the samples.

Analyses of colloidal and non-colloidal carbohydrates were made on all samples collected. Non-colloidal carbohydrates were extracted by repeated steeping in 80 per cent. alcohol and cleared with neutral lead acetate. Total sugars, sucrose, and reducing sugars were determined by the Munson-Walker-Bertrand method in accordance with procedures outlined by LOOMIS and SHULL (**23**). The dry residue from these samples were weighed accurately. They were then ground in a burr mill and the pulverizing completed in a mortar to pass a 200-mesh screen. Duplicate one-gram samples were extracted with hot water to remove soluble colloidal carbohydrates. The cleared extractions were hydrolyzed with dilute hydrochloric acid in an autoclave and determinations of glucosans and levulosans made according to procedures outlined by LOOMIS and SHULL (**23**). All calculations were converted to a green-weight basis.

STUDIES OF SOIL TEMPERATURES ON HEAVILY-GRAZED AND PROTECTED AREAS

Soil temperatures were taken at different depths on heavily-grazed and on ungrazed areas to determine the effect of vegetative cover on soil temperature. Studies were made on a semi-desert grassland type near Alamogordo, New Mexico, in early July of 1941. A protected area was selected along a railroad right-of-way which supported a good stand of grass, chiefly alkali sacaton [*Sporobolus airoides* (Torr.) Torr.]. Just through the fence a contrasting area was selected which had been heavily grazed until only about one-tenth of the original grass cover remained.

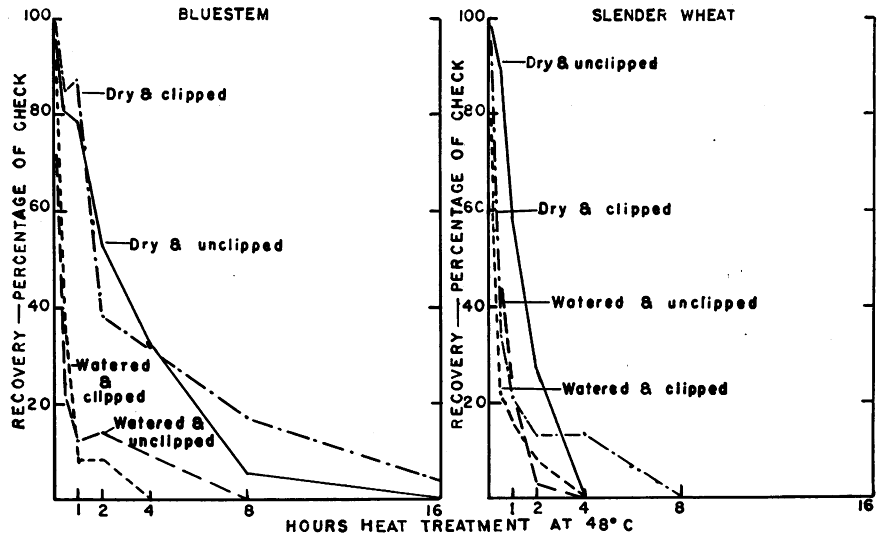
Three thermometers were placed on each area at each of the following depths: surface ($\frac{1}{2}$ of mercury above ground), $\frac{1}{2}$, 1, 2, 4, and 8 inches. The three thermometers of the same depth were located; one in the center, one 4 inches from the edge of the crown, and one half way between two typical grass clumps. Holes the same size as the thermometer were carefully made, slightly deeper than the desired depth. A little loose soil was poured in to serve as a cushion in which the bulb could be buried without breaking. The thermometers were then inserted to the desired depth. A wooden holder protected the thermometer from the direct rays of the sun. This holder was bolted to a strap iron peg which was bent to provide a 6-inch offset so the peg would not interfere with the soil adjacent to the thermometer. This offset was always placed to the south and the position of the wooden holder adjusted to shade the thermometer at mid-day without shading the soil where the thermometer was inserted.

Thermometers protected from the direct rays of the sun were located one foot above ground for air temperatures. Readings were made at hourly intervals for three consecutive days. Similar soil temperatures were taken on heavily-grazed and protected bluegrass sod at a 7,500-foot elevation in the Lincoln National Forest of New Mexico. The experiment was repeated also on the clipped and unclipped wheatgrass plots in the North Ogden, Utah, cemetery (fig. 5A) in August, 1941.

Results

RESISTANCE OF CROWNS AND RHIZOMES TO HIGH TEMPERATURES

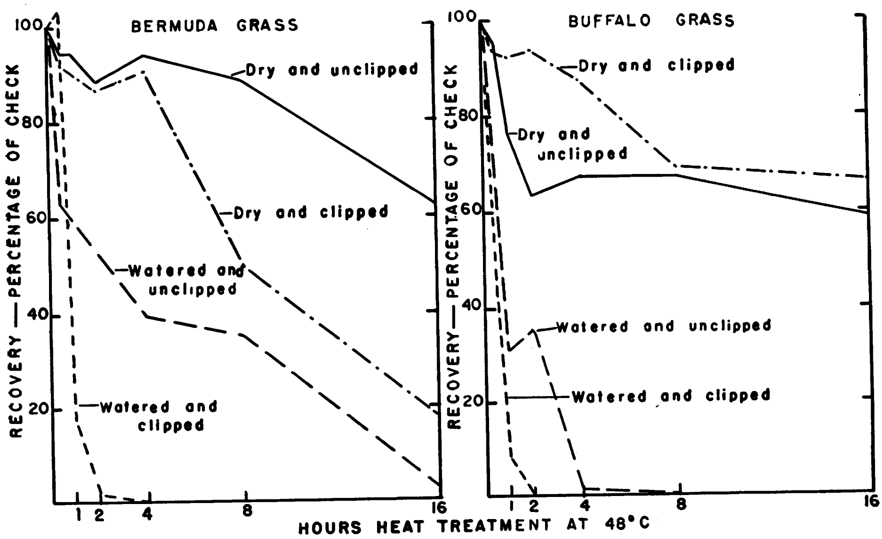
HEAT RESISTANCE OF DIFFERENT SPECIES.—The fact that some species of grass thrive naturally in areas of high temperatures while others are found only in the cooler sites, suggests a difference in their ability to withstand



FIGS. 1 and 2. Recovery of bluestem and slender wheatgrass, with varying previous treatment, after heating at 48° C.

high temperatures. The previous hardening treatments given the grasses would also be expected to influence their heat resistance. Both expectations are supported by the data of figures 1 to 4 which show the recovery of four grass species with varying hardening treatments from exposures to a temperature of 48° C.

Little difference was observed in the heat resistance of the four species in the unhardened condition. When the grasses were watered and clipped,



FIGS. 3 and 4. Recovery of Bermuda and buffalo grasses, with varying previous treatment, after heating at 48° C.

producing unhardened plants with very low food reserves, all species were killed readily. In the watered and unclipped series Bermuda grass stood out as the more heat resistant, with indications that buffalo grass in this condition was slightly more resistant than the two wheat grasses. Drought-hardened Bermuda and buffalo grasses were able to withstand considerably more heat exposure than the other two species (figs. 3, 4). Slender wheatgrass was apparently the least resistant of the four species with bluestem wheatgrass in an intermediate position.

Although moisture and clipping treatments were not randomized, the species were, and an analysis of variance of the data brings out the important comparisons (table I). According to this analysis the difference between species was highly significant, and species, and interactions in which species were involved, account for a high percentage of the total sum of squares.

TABLE I

ANALYSIS OF VARIANCE OF HEAT TREATMENT DATA

SOURCE	SUM OF SQUARES	DF	MEAN SQUARES
Total	137,100	223	
Moisture	19,389	1	19,389.00*
Species	29,730	3	9,910.00*
Moisture × species	12,823	3	4,274.33*
Clipping	2,238	1	2,238.00*
Moisture × clipping	254	1	254.00*
Species × clipping	3,173	3	1,057.67*
Moisture × species × clipping	583	3	194.00*
Treatment	51,569	6	8,594.83*
Moisture × treatment	6,302	6	1,050.34*
Species × treatment	2,570	18	142.77*
Moisture × treatment × species	2,565	18	142.51*
Clipping × treatment	217	6	36.17*
Moisture × clipping × treatment	832	6	138.67*
Species × clipping × treatment	1,470	18	81.67*
Moisture × species × clipping × treatment	2,041	18	113,39*
Error	1,341	111	....
Replications	3	1	....
Total error (error + replications)	1,344	112	12.00

* Significant at the 1 per cent. level.

Kentucky bluegrass (*Poa pratensis* L.), either from field plats or with greenhouse treatments similar to those used in the above experiment, was quickly killed by 48° C. and a temperature of 45° C. was used to show the greater heat resistance of previously hardened plants. Listed in order of heat resistance, Bermuda and buffalo grasses stand out as very resistant, bluestem as intermediate, slender wheatgrass and smooth brome as low, and Kentucky bluegrass as the least resistant. These results agree with field observations. In the hot regions of the Southwest bluegrass is used for lawns only under the protection of partial shade while Bermuda grass thrives in full sunlight. SAVAGE (**36**) lists buffalo grass as the most drought resistant species on the Great Plains and states that although bluestem was mostly killed out, it withstood drought better than most tall grasses. Bluestem, while not found in the low, hot deserts of the Southwest, extends well down into the foothills. It also thrives in the semi-desert sagebrush-grass types of the Great Basin and through the Great Plains where temperatures are moderately high. Slender wheatgrass does not extend as far down the mountains into the hot, arid regions nor as far south in the Great Plains as does bluestem. It thrives best at moderate elevations in the mountains and on the northern Great Plains.

The ability of these grasses to withstand heat is apparently an important factor in determining their natural habitat. Heat resistance also appears to be an indication of the drought resistance of the grasses studied. Judging from their natural habitat they would fall in the same order when listed according to drought resistance as when listed according to their heat resistance. Kentucky bluegrass is much less drought resistant than the other species tested, followed by slender wheatgrass and smooth brome, with bluestem intermediate and buffalo grass outstanding in drought resistance. The only question is with respect to Bermuda grass which grows chiefly in areas of fairly high annual precipitation. In such areas, however, rainfall distribution is often uneven and severe drought periods are not uncommon. Bermuda grass survives these drought periods and has the reputation of being one of the most drought-resistant grasses in its native range.

Relation of clipping and drought to heat resistance.—The curves of figures 1 to 4 and the analyses of table I also contain the data on the effect of clipping and watering treatments on heat resistance. Clipping reduces the photosynthetic area, and watering favors the use of carbohydrates in growth. The unclipped and sparingly-watered plants would have been expected, therefore, to accumulate a greater percentage of carbohydrates. Data to be presented later show that such an accumulation occurred in both the greenhouse experiments and in unclipped or ungrazed grasses in the field during drought. Carbohydrate accumulations should stimulate the differentiation (hardening) of protoplasm (**14**, **15**, **22**, **44**) and thus its resistance to heat. The data presented indicate that hardening was a major factor in heat resistance. In all instances hardened plants were more resistant to heat than unhardened plants. The least difference was with slender wheatgrass. The probable reason for the lack of hardening in this species was its rather poor condition toward the close of the drought treatment; apparently the greenhouse temperature was too high. This effect tended to complicate the analyses of variance of the data. Nevertheless moisture condition accounted for a greater percentage of the total mean square than any other single factor (table I). Also, all interactions in which moisture was represented had a fairly large mean square.

Drought-hardened plants were more sturdy and tough. The rhizomes and crowns had considerably more outward protective cover in the form of scales. Microscopic examination revealed more lignification in hardened plants, as would be expected (**22**). The protoplasm may be assumed to have possessed the hardened qualities common to drought or frost-hardened plants as found by several workers (**20, 21, 22, 38, 39**), which enabled them to resist heat to a greater extent than unhardened plants.

In the analyses of variance of the clipping and drought-treatment data, the effects of clipping proved highly significant by the F test (**9**). However, the magnitude of the mean square for clipping was far less than for species, moisture, or heat treatments. Two factors reacted to complicate the data in this analysis: (a) Bermuda and buffalo grass stool out near the ground when clipped, thereby retaining a considerable volume of foliage for manufacturing food supplies necessary in the hardening process; (b) the unclipped plants had to be clipped to a 4-inch height during the heat treatment. This severe clipping of these tall plants deprived them of the food-manufacturing ability necessary for rapid recovery. The injury was especially great for the two wheatgrasses which have sparse basal leaves. Considerably greater difference would probably have been shown in the heat resistance of clipped and unclipped plants had it not been for these effects.

RELATION OF GRAZING TO HEAT RESISTANCE.—The results of heat treatments of Kentucky bluegrass rhizomes collected from a heavily grazed pasture and from an adjacent protected area showed a decided difference in their ability to resist heat. Clipping supposedly has the same effect as grazing and is used to simulate grazing. No trampling is done in clipping, however, and the results of a two-month clipping do not show the accumulative effects of continued heavy grazing. Other factors, such as compacting of the soil, erosion, less water infiltration, less water-holding capacity, and the competition of ungrazed plants also act to the disadvantage of heavily grazed plants as compared to artificially clipped plants. Still another important factor working to the detriment of heavily grazed plants is the limited root and rhizome development of such plants (**3, 17, 41, 45**). Although clipping has similar effects on root and rhizome development, the result in short time experiments might be less severe than on heavily grazed range.

CARBOHYDRATE RESERVES

EFFECT OF CLIPPING AND DROUGHT TREATMENTS ON RESERVES.—Table II contains the averages of the carbohydrate analyses of Bermuda and buffalo grasses grown in the greenhouse under four different conditions (figs. 3 and 4 and table I). Sufficient material was not available for carbohydrate analyses of the other grasses used in the heat treatment experiment. Although the data are limited they give a good indication of the effect of clipping and water supply on the food reserves of the grasses tested.

Unclipped, drought-treated plants of Bermuda grass showed a greater accumulation of carbohydrate food reserves than plants of any of the other treatments. The difference between the two drought treatments was chiefly in the amounts of colloidal carbohydrates in the form of glucosans and reducing sugars. There was a steady decline in reducing sugars from the unclipped, dry treatment down to the clipped and watered. Differences were not so noticeable in sucrose content. There were distinct differences in the quantity of colloidal carbohydrates stored in the four treatment lots, but the most significant difference lay in the spread between the reserves of drought-treated and watered plants. Differences were found between clipped and unclipped watered plants in all of the carbohydrate fractions. Most of these differences were statistically significant in spite of the variability of the material.

With buffalo grass the food reserve differences were chiefly between dry and watered plants although consistent differences for all carbohydrate fractions occurred between clipped and unclipped, watered plants as in Bermuda grass. The chief difference indicated for clipped and unclipped, dry

TABLE II

AVERAGES OF CARBOHYDRATE ANALYSES OF ROOT AND RHIZOME SAMPLES OF BERMUDA GRASS AND BUFFALO GRASS*

Species and treatment	Non-colloidal carbohydrates			Colloidal carbohydrates	Total carbohydrates
	Reducing sugars	Sucrose	Total non-colloidal	Glucosans	
Bermuda grass					
Dry and unclipped	245 ± 16	3868 ± 32	4114 ± 15	2737 ± 368	6841 ± 384
Dry and clipped	154 ± 4	3975 ± 86	4129 ± 82	1553 ± 368	5682 ± 287
Watered and unclipped	122 ± 22	3199 ± 90	3321 ± 68	326 ± 90	3648 ± 157
Watered and clipped	68 ± 12	2502 ± 166	2570 ± 154	224 ± 60	2794 ± 213
Buffalo grass					
Dry and unclipped	405 ± 13	4779 ± 535	5185 ± 548	650 ± 123	5884 ± 721
Dry and clipped	404 ± 50	4977 ± 815	5381 ± 865	416 ± 56	5797 ± 810
Watered and unclipped	254 ± 26	3393 ± 191	3647 ± 217	151 ± 75	3799 ± 291
Watered and clipped	195 ± 37	2386 ± 15	2581 ± 22	128 ± 61	2709 ± 39

* Milligrams per 100 grams green weight of tissue and standard error of the averages.

plants lay in the glucosan content which decreased consistently from the unclipped, dry plants down to the clipped, watered treatment. Buffalo grass showed considerably less accumulations of colloidal carbohydrates than did Bermuda grass. Negative results were obtained in fructosan tests for both grasses. Temperatures under which the plants were grown in the greenhouse were kept high for purposes other than this investigation. Respiration was therefore high and the accumulations of food reserves were probably less than would have been obtained with lower temperatures.

EFFECT OF GRAZING AND DROUGHT ON FOOD RESERVES OF RANGE GRASSES IN OREGON.—The data of tables III and IV show the effect of heavy and moderate grazing and drought on two important range grasses in Oregon. Samples collected before drought were from green but fully mature plants. Those collected after drought were from plants whose leaves had been dried by drought for several weeks.

The outstanding fact revealed is that moderately grazed, bluebunch wheatgrasses stored up large quantities of colloidal carbohydrates as it

TABLE III

AVERAGES OF CARBOHYDRATE ANALYSES OF ROOT SAMPLES OF BLUEBUNCH WHEATGRASS ON HEAVILY GRAZED AND MODERATELY GRAZED RANGE, BEFORE AND AFTER DROUGHT*

Condition	Non-colloidal carbohydrates			Colloidal carbohydrates			Total colloidal and non-colloidal
	Reducing sugars	Sucrose	Total non-colloidal	Levulosans	Glucosans	Total colloidal	
Moderately grazed before drought	374 ± 26	916 ± 76	1290 ± 76	1232 ± 308	1138 ± 226	2371 ± 641	3661 ± 652
Moderately grazed after drought	570 ± 62	1156 ± 54	1726 ± 71	4356 ± 52	1862 ± 342	6219 ± 382	7945 ± 387
Heavily grazed before drought	400 ± 10	710 ± 93	1110 ± 30	178 ± 48	700 ± 117	878 ± 72	1988 ± 92
Heavily grazed after drought	430 ± 23	1351 ± 81	1781 ± 57	448 ± 48	921 ± 160	1370 ± 158	3151 ± 165
T values—11 degrees of freedom							
Moderately grazed before drought compared to after drought	+ 2.92†	+ 2.59†	+ 4.18‡	+ 8.66‡	+ 1.77	+ 5.15‡	+ 5.64‡
Heavily grazed before drought compared to after drought	+ 1.20	+ 5.21‡	+ 10.42‡	+ 3.90‡	+ 1.11	+ 2.81†	+ 6.69‡
Moderately grazed after drought compared to heavily grazed after drought	− 2.11	+ 1.97	+ 0.60	− 55.1‡	− 2.47†	− 11.7‡	− 11.4†

* Milligrams per 100 gm. green weight of roots and standard errors of the averages.
† Significant at the 5 per cent. level (T = 2.20).
‡ Significant at the 1 per cent. level (T = 3.11).

entered the drought period (table III). Nearly ten times as much levulosan was found in the roots of moderately grazed plants after drought as in heavily grazed plants. Glucosan content was approximately twice as great in moderately grazed plants, and total colloidal carbohydrates were over four and one-half times as great. No significant differences in non-colloidal carbohydrates were found between heavily grazed and moderately grazed plants after drought. Sugars accumulated in both treatments; these increases, however, were of small magnitude compared to increases in levulosans. No significant increase of glucosans was made in either moderately or heavily grazed plants during drought, but this fraction was significantly low in the closely grazed plants.

Bluebunch fescue (*Festuca idahoensis* Elmer), on the same range as bluebunch wheatgrass, showed smaller accumulations of food reserves during drought (table IV). Levulosans increased significantly in moderately grazed plants and showed a slight decrease in heavily grazed plants. Increase in sucrose during drought was highly significant in moderately grazed plants, while a significant decrease was shown in heavily grazed plants. There were no important changes in reducing sugars. Glucosans made significant increases in heavily grazed plants only.

When food reserves of the moderately and heavily grazed plants were compared at the close of the drought period, all carbohydrate fractions were much higher in the moderately grazed plants. As adjudged by the T-test the differences were all significant at the 1 per cent. level. In moderately grazed plants reducing sugars were approximately twice as great, sucrose was about one and one-half times as great, glucosans nearly one and one-third times as great, and levulosans about 17 times the amount contained in heavily grazed plants. This great difference in levulosan content suggests that it may have a special significance in drought resistance of this plant.

Effect of clipping and drought on Virgin Range grasses in Utah.—The data of tables V and VI show the effect of one season's clipping and drought on the food reserves of bluestem and bluebunch wheatgrass growing on a virgin sagebrush-wheatgrass range of Utah. All plots in this investigation were in the same condition at the beginning of the experiment. The plots were side by side on the same exposure, elevation and soil type. Conditions on all plots were as near alike as could be obtained under field conditions, and all sampling was randomized. The data present a clear record of the effects of clipping and drought during one season. Figure 5A shows a part of the area used; figure 5B shows adjacent over-grazed range.

Differences in food reserves brought about by drought alone were highly significant increases of large magnitudes in all carbohydrate fractions except reducing sugars which showed a highly significant decrease. Apparently the reducing sugars not used in respiration were converted into more complex carbohydrates during drought. The larger food reserve accumulations were in the form of colloidal carbohydrates—both levulosans and glucosans. Indications are that sucrose also was stored as reserve food. Food reserve

TABLE IV

AVERAGES OF CARBOHYDRATE ANALYSES OF ROOT SAMPLES OF BLUEBUNCH FESCUE UNDER HEAVY AND MODERATE GRAZING, BEFORE AND AFTER DROUGHT*

Condition	Non-colloidal carbohydrates			Colloidal carbohydrates			Total colloidal and non-colloidal
	Reducing sugars	Sucrose	Total non-colloidal	Levulosans	Glucosans	Total colloidal	
Moderately grazed before drought	630 ± 90	592 ± 61	1222 ± 91	128 ± 28	1325 ± 71	1452 ± 49	2674 ± 134
Moderately grazed after drought	472 ± 16	1146 ± 61	1618 ± 49	275 ± 44	1451 ± 10	1726 ± 41	3344 ± 81
Heavily grazed before drought	213 ± 22	852 ± 18	1065 ± 24	43 ± 14	939 ± 19	982 ± 27	2047 ± 13
Heavily grazed after drought	227 ± 24	761 ± 30	988 ± 44	16 ± 10	1130 ± 48	1146 ± 47	2134 ± 66
T VALUES—11 DEGREES OF FREEDOM							
Moderately grazed before drought compared to after drought	− 1.73	+ 6.42‡	+ 3.83‡	+ 2.82†	+ 1.75	+ 4.28‡	+ 4.27‡
Heavily grazed before drought compared to after drought	+ 0.42	− 2.56†	− 1.53	− 1.57	+ 3.70‡	+ 3.02†	+ 1.29
Moderately grazed after drought compared to heavily grazed after drought	− 8.50‡	− 5.95‡	− 9.57‡	− 5.75‡	− 6.55‡	− 9.33‡	− 11.6‡

* Milligrams per 100 gm. green weight of roots and crowns and standard errors of the averages.
† Significant at the 5 per cent. level (T = 2.20).
‡ Significant at the 1 per cent. level (T = 3.11).

TABLE V

AVERAGES OF CARBOHYDRATE ANALYSES OF ROOT AND RHIZOME SAMPLES OF BLUESTEM FROM VIRGIN RANGE BEFORE DROUGHT AND FROM CLIPPED AND UNCLIPPED PLOTS AFTER DROUGHT*

CONDITION	NON-COLLOIDAL CARBOHYDRATE			COLLOIDAL CARBOHYDRATE			TOTAL COLLOIDAL AND NON-COLLOIDAL
	REDUCING SUGARS	SUCROSE	TOTAL NON-COLLOIDAL	LEVULOSANS	GLUCOSANS	TOTAL COLLOIDAL	
Virgin before drought	351 ± 6	468 ± 25	819 ± 21	1066 ± 78	1227 ± 33	2282 ± 51	3111 ± 65
Virgin after drought	239 ± 7	1999 ± 44	2243 ± 32	3418 ± 75	3090 ± 151	6508 ± 190	8752 ± 236
Clipped plots after drought	242 ± 4	831 ± 13	1073 ± 12	216 ± 31	1278 ± 39	1494 ± 14	2568 ± 41
T VALUES—5 DEGREES OF FREEDOM							
Virgin before drought compared to virgin after drought	−12.2†	+30.0†	+32.6†	+21.8†	+12.1†	+21.9†	+23.0†
Virgin before drought compared to clipped after drought	−15.1†	+12.4†	+10.5†	−10.1†	+ 1.0	−16.1†	− 7.1†

* Milligrams per 100 gm. green weight of roots and rhizomes with standard errors.
† Significant at the 1 per cent. level (T = 4.032).

TABLE VI

AVERAGES OF CARBOHYDRATE ANALYSES OF ROOT SAMPLES OF BLUEBUNCH WHEATGRASS FROM VIRGIN RANGE BEFORE DROUGHT AND FROM CLIPPED AND UNCLIPPED PLOTS AFTER DROUGHT*

CONDITION	NON-COLLOIDAL CARBOHYDRATE			COLLOIDAL CARBOHYDRATE			TOTAL COLLOIDAL AND NON-COLLOIDAL
	REDUCING SUGARS	SUCROSE	TOTAL NON-COLLOIDAL	LEVULOSANS	GLUCOSANS	TOTAL COLLOIDAL	
Virgin before drought	234 ± 7	529 ± 31	763 ± 25	1334 ± 116	1437 ± 29	2771 ± 108	3534 ± 143
Virgin after drought	191 ± 5	1272 ± 18	1463 ± 12	2900 ± 157	3066 ± 116	5950 ± 125	7414 ± 131
Clipped plots after drought	241 ± 2	810 ± 4	1050 ± 2	1043 ± 47	1652 ± 97	2695 ± 149	3746 ± 154
T VALUES—5 DEGREES OF FREEDOM							
Virgin before drought compared to virgin after drought	− 5.07†	+ 20.7†	+ 25.3†	+ 8.04†	+ 13.6†	+ 19.5†	+ 19.9†
Virgin before drought compared to clipped after drought	+ 0.96	+ 9.0†	+ 11.4†	− 2.32	+ 2.11	+ 0.41	+ 0.95

* Milligrams per 100 gm. green weight of roots with standard errors.
† Significant at the 1 per cent. level (T = 4.032).

accumulation and the formation of colloidal carbohydrates during drought was the same for bluestem and bluebunch wheatgrass. The data from these species agree in general also with that presented earlier for the other grasses included in this study.

The striking result of clipping combined with drought was the prevention of any build-up of either levulosans or glucosans. In the clipped bluestem plants levulosans not only failed to increase during drought but dropped to 20 per cent. of their original value. The only significant increase in clipped

FIG. 5. Above—virgin sagebrush-wheatgrass range near Ogden, Utah; abundant wheatgrass and scattered sagebrush. Below—adjoining, over-grazed area; mostly sagebrush and downy chess.

plants of either species during drought was in the amount of sucrose present. Clipped bluestem after drought showed less than one-third as much total carbohydrate as unclipped plants. With clipped bluebunch wheatgrass the total carbohydrates were less than half those of the unclipped plants. Colloidal carbohydrates totaled over four times as much in unclipped bluestem as in clipped plants and the difference was more than twice in bluebunch wheatgrass. Colloidal carbohydrates are often reported as starch in the analyses of grass samples. Close microscopic examinations of all species analyzed were made under polarized light. Starch grains were observed in several of the grasses, but they were extremely rare. The formation of starch seems to be possible in grasses, but in the species studied it was not an important form of carbohydrate storage in the vegetative organs. Iodine tests were negative for starch but indicated the common occurrence of dextrins in the grasses studied. These findings agree with those of VASSILIEV and VASSILIEV (**44**) who found starch present in the vegetative organs of wheat but in very small amounts.

EFFECT OF VEGETATIVE COVER ON SOIL TEMPERATURES

The results of the heat resistance studies prompted a third series of experiments. Since over-grazing is closely associated with drought injury,

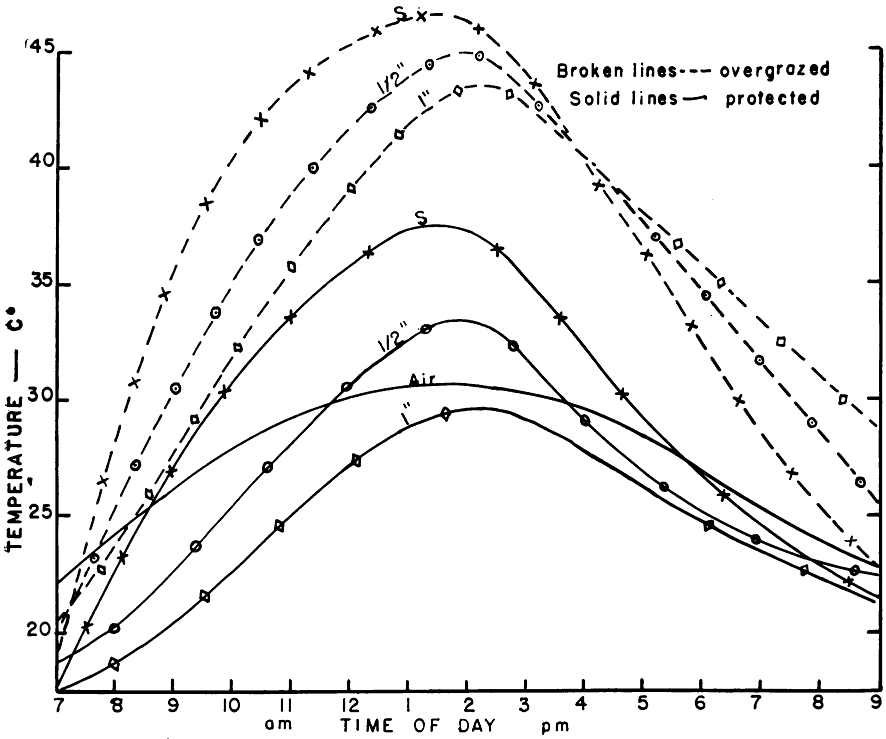


FIG. 6. Soil temperatures at 0- to 1-inch depths on over-grazed and protected, semi-desert grassland.

and clipped plants were less resistant to heat, it is possible that the reduced soil protection on an over-grazed range may contribute directly to grass injury by allowing higher soil temperatures. These effects would be in addition to the reduced resistance of closely grazed plants and would compound the injurious effects of overgrazing. Preliminary measurements on a mountain, bluegrass range showed soil temperatures in closely grazed areas several degrees higher than where the grass covering was less disturbed. Measurements on clipped and unclipped virgin range in Utah showed soil temperature differences of nearly 10° C. Measurements under more critical conditions were obtained on a semi-desert range in New Mexico.

SOIL TEMPERATURES ON OVER-GRAZED AND PROTECTED SEMI-DESERT GRASSLAND OF NEW MEXICO.—The semi-desert grass plots were selected to obtain typical over-grazed range for comparison with the same type range in good condition. The protected plot along a railroad right-of-way had a good stand of alkali sacaton (*Sporobolis airoides*), with an average vegetative soil cover of about 65 per cent. The over-grazed plot just through the fence supported only about one-tenth as much vegetative cover, and part of this was undesirable weeds and half-shrubs. The over-grazed plots differed further in having from one to two inches of top soil lost by recent erosion, as indicated by the heights of grass pedestals. Soil on the protected area had more pro-

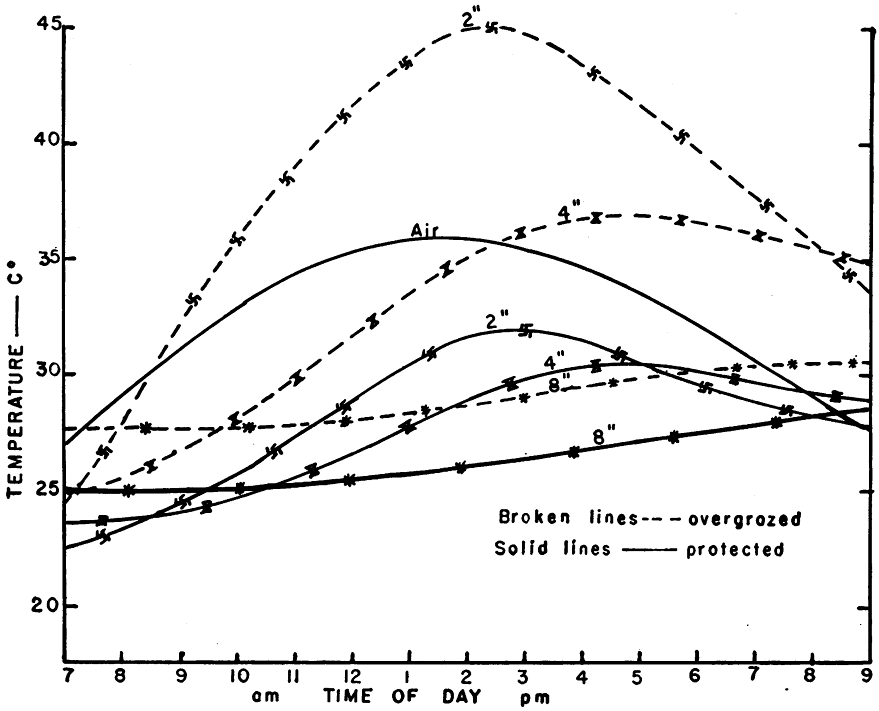


FIG. 7. Soil temperatures at 2- to 8-inch depths on over-grazed and protected, semi-desert grassland.

tective cover in the way of undecayed dead vegetative matter as well as greater organic material in the top soil.

Figures 6 and 7 show three-day average soil temperatures on over-grazed and protected, semi-desert grass plots and present a graphic comparison of the soil temperatures at various depths and the air temperatures at different times of day. Figure 6 compares the soil temperatures at surface, ½-inch, and 1-inch depths. In all cases temperatures on the over-grazed areas were considerably higher. Maximum soil temperatures for the day on the over-grazed surface were about 9 degrees higher, at the ½-inch depth over 11 degrees higher, and nearly 14 degrees higher at the 1-inch depth than temperatures at similar depths on the protected area. At the 2-inch depth (fig. 7) soil temperatures averaged about 13 degrees higher on over-grazed range. At the 4-inch depth a difference of about 6½ degrees at 4 or 5 P.M. was found. At the 8-inch depth, temperatures between over-grazed and protected areas differed about 3 degrees throughout the day. Not only were soil temperatures higher on the over-grazed area, but the high temperatures extended over a longer period of time because they rose much more rapidly in the morning and declined less rapidly in the evening. A wide difference in soil temperatures therefore existed from shortly after sunrise until after sunset.

There was a distinct lag in the time at which different soil depths reached maximum temperatures during the day. Surface temperatures reached their maximum between 1 and 2 P.M. at the time of maximum air temperatures. Maximum temperatures for other depths were as follows: 2 P.M. for the ½-inch depth; about 2:30 P.M. for the 1-inch depth; between 2 and 3 P.M.

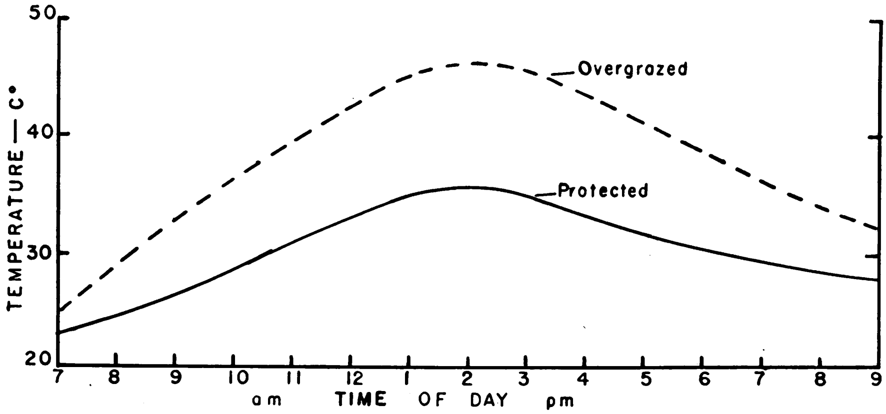


FIG. 8. Average soil temperatures for 0- to 4-inch depths on over-grazed and protected, semi-desert glassland.

for the 2-inch depth; about 5 P.M. for the 4-inch depth; and not until 8 or 9 P.M. for the 8-inch depth.

Soil temperatures on the over-grazed area from the surface to the 2-inch depth were much higher than air temperatures, reaching what are commonly considered lethal or near-lethal temperatures for plants, especially at the surface, ½-inch, and 1-inch depths where they reached a maximum of 51.5, 50.0, and 48.5° C., respectively. Even at the 4-inch depth, soil temperatures reached a higher maximum than air temperatures. Soil temperatures on the ungrazed area were below air temperatures except at the surface and ½-inch depths. Even these shallower depths did not reach dangerously high maxima. Figure 8 gives a comparison between average temperatures for the first four inches of soil on over-grazed and protected areas. A substantial difference is shown throughout the day and as much as 10° C. at midday.

Temperature and other drought conditions were not excessive during the period of study. Maximum air temperatures were slightly under 36° C. (96.8° F.), whereas during periods of severe drought temperatures of over

43.35° C. (110° F.) are not uncommon. SAVAGE (**36**) reported that the average maximum temperature for a sixty-day period at Woodward, Oklahoma, was 100.6° F. during the summer of 1934. At higher air temperatures the soil temperatures should be proportionately greater. Air temperatures of 100° F. and over could be expected to result in soil temperatures reaching a critically high stage to a 4-inch depth and maintaining it for a period of several hours each day.

On the semi-desert area studied, most of the grass roots occurred in the first six inches of soil, although a few roots reached a depth of several feet. Root-crowns and stolons are at or near the ground surface, and most grass rhizomes are in the first inch of soil. These vital plant parts, as well as the mass of feeder roots, are exposed to high soil temperatures in periods of hot weather and drought. This exposure is undoubtedly an important factor contributing to the high mortality of grasses during drought years.

Differences in soil temperatures on over-grazed and protected range as shown in this investigation are sufficient to affect greatly the rate of respiration and other vital processes within plants. Temperatures on over-grazed range reached levels which have been reported lethal to other plants. Such temperatures were higher than those which killed heavily grazed grasses in experimental heat treatments previously reported in this study (figs. 1 and 4). It is very reasonable, therefore, to assume that the high soil temperatures reached during drought on over-grazed range may be a direct cause of death of forage plants.

Discussion

The survival of different species on semi-desert ranges subjected to heavy grazing may be determined by the growth form and other natural adaptation of the plants to withstand close cropping, as well as by their inherent ability to resist heat and dehydration. Drought-resistant, tall or mid-grasses of the bunch type are often replaced by short grasses or sod-forming grasses which are better able to resist heavy grazing. On the Coconino Plateau of northern Arizona blue grama has replaced the climax bunch-grasses on heavily grazed mountain parks. The results of this study indicate that the greater drought resistance of such short grasses on heavily grazed, arid ranges may be due largely to their ability to maintain a considerable photosynthetic area, for manufacturing food reserves for protoplasm hardening in spite of close grazing.

Critically high temperatures generally accompany extended drought and injure forage plants by: (a) increasing respiration, and thus increasing food requirements; (b) increasing transpiration and evaporation which decreases the amount of water available; and (c) causing direct heat injury or death. Since respiration is increased by high temperatures during drought, a good supply of reserve food is necessary to support respiration as well as to enable roots, crowns, and rhizomes to become hardened to withstand heat and dehydration. McCARTY (**26**) and McCARTY and PRICE (**27**) have emphasized the necessity of limiting fall grazing to permit autumn food reserve storage for winter hardiness and for vigorous spring growth. On semi-desert ranges, drought is much more destructive than frost. Food storage for drought hardening is therefore even more important than reserves for winter hardiness in these areas.

The results of this study emphasize the importance of moderate grazing before drought. Such practice permits accumulation of food reserves for drought hardening and the residual vegetation forms a protective cover which prevents excessive soil temperatures and reduces run-off and erosion. The result is less severe drought conditions together with hardened plants which are better able to resist heat and dehydration and are capable of rapid recovery with the return of good growing conditions. Over-grazing on arid ranges initiates a vicious cycle. The more a range is over-grazed the more severe drought conditions become and the less are forage plants able to resist heat and dehydration. Increased competition of unpalatable non-forage plants adds further complications to drought survival on over-grazed range. Still another serious handicap of over-grazed plants is the limiting of root growth by close cropping (**45**). LANTOW and FLORY (**17**) estimated that blue grama grass roots in full vigor had a root penetration of $2\frac{1}{2}$ to $3\frac{3}{4}$ feet. Those of low vigor reached a depth of 1 to $2\frac{1}{2}$ feet with an estimated volume of $\frac{1}{3}$ that of full vigor roots. Plants of depleted vigor had a root depth of $\frac{1}{2}$ to $\frac{3}{4}$ feet with only about $\frac{1}{10}$ of the root volume of full vigor plants. Not only is root volume and penetration restricted, but the amount of water in the soil is limited because of increased run-off and decreased water holding capacity of the soil resulting from erosion. The above factors working together inevitably result in serious depletion of both forage cover and site conditions.

Regulating grazing to meet plant requirements during drought years is one of the most difficult problems in sustained yield range management. This fact is reflected in the depleted condition of a large proportion of the semi-desert ranges of the west. Growing conditions fluctuate radically from year to year, and drought alone is often severe enough to cause considerable depletion in vegetative cover. Common practice on many private and unregulated ranges during drought is to hold over as many livestock as will live through the dry period without starvation. Such practice works directly contrary to forage plant requirements. The more severe the drought the heavier the chief forage plants are grazed, and the heavier they are grazed the less drought they are capable of withstanding.

Regulating numbers of livestock to meet plant growth requirements is especially difficult on year-long ranges where livestock depend entirely on the range for forage. To meet this problem the U. S. Forest Service recommends stocking and breeding herd on the basis of 10 to 30 per cent. below the carrying capacity of the average year, depending upon the frequency and severity of drought conditions. They also recommend some fluctuating of livestock numbers to meet current changes in forage supply. Under this management the good years are supposed to offset the bad effect of drought years. LANTOW and FLORY (17) of the Soil Conservation Service advise going all the way in fluctuating livestock numbers to meet the current forage supply. Theoretically this system is adapted to meet plant requirements during drought. The practicability of the system is questionable, however, on ranges where supplemental feed is not available at a reasonable cost. On some ranges of the Southwest practically no growth is made during extreme drought years. To meet survival requirements of key forage plants no grazing should be permitted during such years and no breeding stock could be carried over. The system of fluctuating livestock to meet current forage supplies is very desirable from the standpoint of plant requirements and is good practice as far as practical application permits.

The results of this study confirm, from a drought-resistance standpoint, the soundness of some of the main principles of range management as developed by the U. S. Forest Service; namely, the practice of moderate grazing, proper season of use, and deferred and rotation grazing. Deferred and rotation grazing as commonly practiced on national forest ranges to insure seed production and natural reproduction is also beneficial in drought resistance. When grazing is deferred until after seed maturity the plants are in good condition to resist drought. Since the deferring of grazing is rotated from year to year on different units, the entire range benefits from a drought-resistance standpoint. CRADDOCK and FORSLING (8), working on a spring-fall sheep range of southern Idaho, found that the deterioration in the vegetative cover of important forage plants varied directly with the intensity of early spring grazing. This area is subjected to frequent droughts, and in this case too-early grazing was apparently an important factor contributing to drought destruction of the important forage plants.

Application of the results of the carbohydrate studies before and after drought, and of the investigation on the influence of food reserves on heat resistance, to range management calls for special utilization standards for important forage plants on arid ranges to be applied at the beginning of the usual dry period. Leaf area is the key to drought hardiness of forage plants. It is realized that regulating proper use at the beginning of the dry season is not without complicated problems, but drought destruction of major forage plants will be alleviated to the extent to which this practice is followed.

Summary and conclusions

1. A study was made of drought factors affecting range grasses as follows: (a) Heat-resistance tests were made with five grasses grown under four different conditions to determine the effect of food reserves on heat resistance. Supplementary tests were also made with heavily grazed, clipped, and protected plants grown in the field. Plants, protected by glass tubes, were immersed in a constant-temperature bath and exposed for ½ to 16 hours to a temperature of 48° C.; (b) Carbohydrate analyses were made of root and rhizome samples of range grasses to determine the effect of heavy grazing and clipping upon food reserves before and after drought,

and to investigate the rôle of the various carbohydrate fractions in drought resistance; (c) Soil temperatures were taken on over-grazed and protected range and on clipped and unclipped virgin range to determine the effect of vegetative cover and over-grazing on soil temperatures.

2. There were highly significant differences in the ability of the grasses tested to resist heat. Buffalo grass and Bermuda grass were most resistant, bluestem was intermediate and slender wheat, smooth brome, and Kentucky bluegrass were low in resistance.

3. Accumulation of food reserves was essential to heat resistance. All species tested when low in food reserves and unhardened were very susceptible to exposures of 48° C. Heat resistance increased with an increase in food reserves.

4. Results of this study indicate that heat resistance is a measure of drought resistance. The ability of the species tested to resist heat corresponds closely with the aridity of their natural habitats. Further tests with additional species are necessary for more definite conclusions.

5. Hardening by drought, under conditions favoring accumulation of reserves, produced highly significant differences in the ability of grasses to resist heat. Drought-hardened plants were much higher in food reserves than unhardened plants and were more resistant to heat injury in all comparisons.

6. The detrimental effects of clipping on heat resistance proved highly significant when the data on all species were pooled. Bermuda grass, buffalo grasses, and bluegrass, however, were much more resistant to clipping than other species. By stooling out near the ground these grasses were able to maintain sufficient foliage, even under moderately heavy clipping, to provide reserve accumulations for drought hardening. Heavy grazing of bluegrass resulted in a decrease in heat resistance.

7. Samples taken before and after drought revealed that protected or moderately grazed grasses accumulated excess food reserves as they entered drought. Large accumulation of colloidal carbohydrates, especially levulosans, was associated with drought resistance. Over-grazed and heavily clipped plants did not accumulate food reserves during drought and were less resistant.

8. Bodies thought to be starch grains were observed in several grasses, but this form of carbohydrate was extremely limited in the species studied. Sucrose accumulations were found whenever large supplies of colloidal carbohydrates were present, but reducing sugars did not accumulate during drought.

9. Several of the chief principles of range management as developed by the U. S. Forest Service are substantiated by the results of this study from a drought-resistance standpoint.

10. Application of the results of this study calls for further adjustments in range management to provide proper utilization standards for important forage plants at the beginning of the usual dry season. Such practice would

provide for: (a) hardened plants capable of withstanding drought; (b) adequate food reserves for respiration and for vigorous recovery after drought; and (c) reduction in drought conditions by a protective vegetative cover which guards against high soil temperatures and water loss.

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