TOLERANCE OF SORGHUM SEEDLINGS TO HIGH TEMPERATURE AND DROUGHT

by

CHI CHEN

B. S., University of Nanking, 1928

A THESIS

submitted in partial fulfillment of the

requirements for the degree of

MASTER OF SCIENCE

Department of Agronomy

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1938

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INTRODUCTION

Drought may be either atmospheric or edaphic. The former is characterized by the hot dry wind in which the temperature rises so high that plants are usually injured and severe desiccation results, while the latter is referred to as the deficiency of moisture in the soil for the normal development and growth, or maintenance of life, of plants therein. The success of farming in regions subject to drought of either form largely depends upon the ability of crop plants to withstand such stress.

This ability has been classified by Shantz (1927) as drought-escaping, drought-evading, drought-enduring, or drought-resisting. According to his definition, all the field crops now grown which are able to withstand drought do so either because they escape drought or evade drought. Plants escape drought by a short and rapid growth period and ripen their seed before the drought sets in. Plants evade drought by restricting the amount of growth or by the efficient and economical use of water in order to delay the finally using up of the limited amount of water present in the soil. However, his classification is not adopted in agronomic literature, so what we commonly refer to as drought-resistance, drought-tolerance, or drought- endurance of crops may mean either drought-escaping or drought-evading, unless specification has been made by the author. In this report those terms (resistance, tolerance, or endurance) are used to refer to the general ability of plants to withstand drought.

It is a well known fact that such ability varies greatly among different species, but investigations made on crops have led to the discovery also of wide variation among varieties of the same crop. Even in the same plant, its resistance may change at different stages of development or growth. Environmental conditions to which the plant is subjected before or during the drought, exercise a profound influence on the resistance of the crop.

Sorghum is noted as a "plant camel" for its ability to withstand drought. It has often been observed that in certain years certain varieties are superior to others. It is of some value to compare the varieties under various controlled conditions, especially varieties grown in remote regions of different environmental conditions.

The purposes of this experiment are: (a) To compare the resistance of Blackhull kafir, Dwarf Yellow milo, and three strains of Kaoliang to the effect of atmospheric drought, (b) To learn whether or not this resistance varies with the age of the plant, (c) To find the influence of variation in soil moisture on the resistance of plants to atmospheric drought exhibited by different varieties of sorghum, (d) To test the possibility of hardening sorghum plants to drought by a pretreatment at moderately high temperature or by a gradually increasing temperature, and (e) To determine if resistance to atmospheric drought is parallel to resistance to edaphic drought or otherwise.

REVIEW OF LITERATURE

Sachs (1864), reviewed by Baker (1929) in conducting experiments on the effects of high temperature on tobacco, pumpkin, corn and other plants, found that the power of resistance to high temperatures varied at different ages. Developing leaves, stems and roots were more easily killed than older ones.

Brounov (1899, 1912), cited by Maximov (1929), found that cereals were most susceptible to drought at the period of rapid growth in length of the internodes before the emergence of the head from the boot. This period is known as a critical period.

Pfeffer (1903), quoted by Berkley and Berkley (1933), noted that plants which appeared unharmed after a short exposure to high temperatures frequently died later as an after effect even under the best external conditions.

Tumanov (1927), cited by Maximov (1929), investigated the wilting endurance of eight varieties of spring wheat by growing them in flower pots which were placed in the open and transferred to a greenhouse at the shooting stage. There they were left unwatered for two weeks, at the end of which period the soil was irrigated. Several days after recovery the percentage of plants surviving was recorded. He found that the resistant varieties survived not lower than about 80 per cent and the susceptible varieties not higher than 50 per cent and this division agreed with the results from field experiments.

The same author (1927) secured the result from experiment on sunflower showing that a single permanent wilting lowered the yield and checked the development of the assimilating surface, but that subsequent wilting caused no injury to the plant.

Newton and Martin (1930), in the report of physico-chemical studies on the nature of drought resistance of crop plants, made an extensive review of past work on the factors affecting drought resistance in plants. Their results from studying the plant juice of several kinds of wheat, barley, rye, grasses, maize, sunflower and cactus, showed the amount of bound water increased in those species known for their drought resistance. They regarded it was the imbibitional pressure of hydrophylic colloids that opposed the abstraction of water as the resisting factor against physiological drought. By testing the moisture content of _Bouteloua gracilis_ which is xerophytic in structure, they concluded that structural modification of the leaves was not effective in controlling the absolute loss of water but was more probably effective in reducing rate of water loss during the initial period of drought, thus allowing the cells time to develop physiological resistance.

Berkley and Berkley (1933) exposed two series of cotton plants 5 to 180 days old to different temperatures in saturated and 69 per cent relative humidity at 50° C. for a time ranging from half a minute to 72 hours. They found the seedlings were less resistant to high temperature than older plants and that all plants were less resistant to heat at high than at the lower relative humidities.

They suggested the cooling effect of transpiration protected the leaves and cotyledons which lost water rapidly during treatment under lowrelative humidity and therefore suffered no injury while the hypocotyl which lost little water during treatment withered entirely after treatment. They attributed the greater injury in the saturated atmosphere to the smothering effect of the water condensed on the plant surface.

Hunter, Laude, and Brunson (1936), by treating 14-day old seedlings of inbred lines of corn in a heat chamber at 140° F. and with a relative humidity of about 30 per cent for 6.5 hours, found the injury to the tested plants was parallel to the injury from drought in the field. The relative order of resistance of the seedlings was the same as the plants in the field, so it was possible to distinguish the drought resistance between different strains by means of the heat chamber treatment.

Aamodt and Johnston (1936), in their report of studies on drought resistance in spring wheat, made a comprehensive review of previous investigations, especially those of Russian workers. Some of them that have a direct bearing on the present experiment are recited here. Beal found germinating seeds of wheat and buckwheat could be dehydrated five times before the percentage of germination was materially reduced, while after the development of leaves, plants were very susceptible to desiccation. For studying the degree of injury to plants by drought, Tumanov estimated the percentage of dead leaves; Kondo used both percentage of dead leaves and reduction of grain yield; while Krasnosselsky-Maximov by exposing cereals to artificial dry wind noted the injury of leaves and reduction in the yield. As to their own experiment, Aamodt and Johnston subjected several varieties of spring wheat at four stages (stooling, shooting, soft and hard dough stages) to atmospheric drought in a chinook machine and to soil moisture deficiency by withholding watering at different stages. Two kinds of soil were used. The result of their experiments showed that plants at the shooting stage were most susceptible to drought, and injury by air drought was greater than soil drought in both stooling and shooting stages. The effect of soil types varied with the stages of growth and the kind of drought. Hardening the plants either by wilting or by pretreatment in the chinook machine for shorter periods made the plants more resistant to air drought. Varietal difference was found in which Kubanka and Pentad were among the most susceptible ones. They remarked that these two varieties, as pointed out by Russian investigators, were resistant to drought only during the period of ripening but not in the initial growth stage. Studying the root systems of four varieties at 16 and 31 days after emergence, there was an indication that the resistant varieties had a highly branched root system.

Vassiliev and Vassiliev (1936), in connection with hardening five varieties of wheat by severe wilting and bringing to recovery by irrigation, made a series of chemical analyses of the cell content at the beginning of the wilting, at permanent wilting, 24 hours after irrigation, and 8 days after recovery. Their results showed that monosaccharides and sucrose increased, and hemicellulose decreased when wilting set in. During permanent wilting sucrose decreased, monosaccharides increased and hemicellulose decidedly increased. After irrigation the water content increased but not so high as in the control, and soluble sugar decreased. Eight days after recovery the water content still was lower than in the control and sucrose and hemicellulose had increased. They suggested that as the result of the hardening, the changed conditions seemed to be permanent. They also emphasized the importance of hemicellulose to drought resistance.

Shirley (1936), working with several species of conifer seedlings of one to four years old for killing temperature in water bath and in the air, concluded that resistance to excessive heat increased with increasing age and increasing size or mass of plant tissue; that tops were more resistant than roots; that little difference in resistance existed among the species tested; and that the external killing temperature for the seedling was higher in the dry air than in the moist air and higher in the moist air than in water. He attributed the last fact probably to the cooling effect of transpiration.

Arndt (1937) exposed the roots of cotton plants grown in the culture solution and in the soil to low and high temperatures. His results for high temperatures showed that for 60 minutes in 60° C. severe injury was caused to the roots either in the solution or in the soil and absorption was interferred with. Plants in the culture solution wilted at 70° C. for 15 minutes but in the soil wilted at 60° C. White areas appeared between the veins of the leaves during the treatment and disappeared when the temperature was reduced to normal, but reappeared as yellow brown regions in which the tissue died. Leaves dropped off within 12 days. Some of the distant roots in culture solution still increased in length but were irregular in diameter. After several days the roots became flaccid and gelatinous. He suggested the killing of the leaves was due to a toxic substance produced in the roots or possibly in the adjacent soil, and that the death of the heated roots and the discoloration of the non-heated stem xylem might be proof of this supposition.

Bayles and his collaborators (1937), in a treatment of five varieties of wheat grown in the greenhouse in artificially produced wind at 92°- 98°F. found significant differences between most resistant and the most susceptible varieties, but little difference was manifested by intermediate varieties. By weighing the relative rate of loss of water from plants at intervals the varieties could be ranked with respect to decreasing rates, but great variation was found between pots that had received low water supply. Some varieties grown in the field at Tucson, Arizona were ranked in about the same order, but those from Pullman, Washington and Moro, Oregon did not conform to the same order.

MATERIAL AND METHODS

The varieties of sorghum used in the experiments were Blackhull kafir and Dwarf Yellow milo from the Agronomy Department of Kansas State College and 6 strains of Kaoliang, No. 8, No. 11, No. 18, No. 19, No. 21, and No. 25, from the rod row test of Yenching University Agricultural Experiment Farm, Pieping, China. It was found in the first test that Kaoliang No. 8, 18, and 19 germinated irregularly and growth was not uniform so they were not used subsequently.

The seeds were sown in 4-inch pots in the greenhouse and the seedlings, if too many, were thinned to 5 plants per pot one week after emergence. When the plants had grown to the proper stage they were treated in a heat chamber. The relative humidity in thechamber was not controlled but it varied only within the range from 20 to 33 per cent. The proper temperature in the chamber had been determined by a preliminary test which included Blackhull kafir, Dwarf Yellow milo and one strain of Kaoliang in four stages of growth. These tests were all done in the afternoon and temperature varied from 120° F. to 142° F.

It was found that 120° F. produced no effect on the plants and above 135° F. caused death of milo and Kaoliang. Although kafir survived, it was severely injured. So 130° F. was determined to be used for the subsequent experiments. However, in the morning treatments at 130° F., 7 of the 8 varieties and strains mentioned above, were killed, while kafir was injured as much as 90 per cent. Therefore, the difference of the effect of the morning and afternoon treatment was recognized and it was decided to use 125° F. for following experiments, and of the four tests, two were to be done in the morning and two in the afternoon. All the plants treated, unless otherwise indicated, were watered to saturation at the evening previous to treatment.

In the first experiment, the different stages of growth of plants used were 9-10 days, 18-19 days, and 25-26 days after planting. Every variety or strain was tested in triplicate pots for one stage. In the spring the plants grew rapidly so at the 18-19 day stage the plant was as large as at 40 days in the winter. Therefore a brief description of the plants at different stages seems necessary here. The plants at 9-10 days after planting in the spring were from one and one-half to three inches in height with two to three leaves; those at 18-19 days were four to five inches high with three to four leaves; while those of 25-26 days were six to eight inches in height with five to six leaves. Kaoliang was usually the tallest while Blackhull kafir the shortest.

In the experiment on the effect of nearly saturated and optimum soil moisture, three pots of either degree of moisture content were used for every variety or strain in one test. The plants in the soil of nearly saturated moisture were watered every two days to the saturation point and at the evening before the treatment every pot was saturated with water; while in the case of the plants in the soil of optimum moisture, water was applied only to moisten the soil slightly every two days and in the evening four days before treatment the soil was saturated with water to insure a uniform distribution of water, and a small amount of water was added to wet the surface of soil just before the test. The plants were used in this experiment 14-15 days after planting.

In the hardening experiment the plants 19 days after planting were treated at a temperature near 110° F. for four hours and the next day they were treated with the control plants which had been kept in normal greenhouse temperature. Six pots of both pretreated and control for each variety and strain were used in the test. The temperature for this test was increased from 103° F. in the morning and 102.5° F. in the afternoon gradually up to 125° F. at which the plants were left for five hours. The interval required to raise the temperature was three hours and fifteen minutes in the morning and only one hour and forty-five minutes in the afternoon test.

In the soil moisture deficiency experiment each variety or strain was grown in four 10-inch pots in each of which were two plants. Five kilograms of air dried soil was added to each pot, the weight of which was previously determined. At the time of seeding two liters of water was applied to each pot and thereafter 500 cc. of water was supplied twice a week. Forty days after planting all plants had grown to the 7 to 8 leaf stage except one pot of kafir which had only six leaves. These pots with plants were weighed again and enough water was added to each pot to make the moisture content of the soil up to 2000 cc. The surface of the soil now was covered with coarse sand about half an inch thick. Twenty-four days after the setting up, one liter of water was added to each pot and all of the pots were saturated the next day. Two days later the percentage of injury was read and recorded.

RESULTS

Injury by Atmospheric Drought

Injury caused by the atmospheric drought was of two types; one was due to the immediate effect and the other due to the after effect. When plants of the advanced stage of growth had been put in the heat chamber for 10 minutes the tips of the higher leaves drooped. This occurred in both resistant and susceptible varieties. Signs of desiccation did not appear until half an hour had passed. Desiccation began at the tip of the leaf and then extended downward. In the broad portion of the leaf the margin suffered first. This suggests that desiccation is largely due to some disturbance in the water balance of the plant. The injury proceeded from high leaves to lower leaves so the basal leaf was usually the last one to dry out. The topmost young leaf, which had just emerged, often survived, but as soon as about half of its total length protruded out of the sheath of the old leaf the unfolded portion always was killed in the case of the susceptible plants. During the treatment the leaves of the plant never rolled nor folded up. When the plant was taken from the chamber it was found that the desiccated portion of the leaf was grayish green and a narrow, irregular, water soaked, translucent band was observed between the fresh and dry parts.

The after effect usually was manifested one day or less after the treatment and continued for one week or even two weeks. Discoloration and desiccation of the fresh portion of the leaf progressed from the previously injured part gradually downward. In the severe case, it extended down to the crown so the whole plant died, while in the more resistant plant it extended only a little distance below the formerly injured part. The later injured portion in contrast to the old grayish green desiccated area was white in color and appeared to be very thin showing that the content in the cell had been disorganized. In plants with the first injury less than 10 per cent, this kind of after effect was seldom found. Sometimes the later desiccation occurred between fresh portions of a leaf or stem. If it happened at the region of the folding sheaths it caused the whole plant to fall down though the part above the lesion was still fresh. In the case of older plants, this phenomenon appeared very late, about one week after the treatment. This may be due to certain injury of the cell during the time of treatment causing the protoplasm to disintegrate and become dry. Injury to roots may contribute some part in such effect, for when most of the roots have died there is an insufficiency of water for the top which causes the gradually drying of leaves. The chance of survival was very little for a plant showing over 60 per cent of injury at the end of the treatment. With the exception of those plants at the earliest stage of growth and those hardened by moderately high temperature, the growth of the surviving plants was retarded for varying lengths of time, according to the degree of injury. This inhibition of growth may be caused by high temperature which so disturbs the metabolism of the plant that it must take time to regain its normal growth. Perhaps the extent to which the roots were destroyed is another determining factor, for it might be assumed that the top will start to grow only after the roots have recovered, and the length of time for the recovery of roots is directly proportional to the degree of injury.

A few observations were made on the injury of the root system. The degree of injury was found to be closely related to that of the top. If one is the cause of another or if they are independent to each other cannot be ascertained until some further investigation is made.

Degree of Resistance of Different Varieties and Strains at Different Ages Treated in the Morning and in the Afternoon

The degree of injury to different varieties at different states of growth in the preliminary test showed that Blackhull kafir was superior to Dwarf Yellow milo in air drought resistance and Kaoliang No. 7 always was the least resistant, while all of them decreased in resistance as their age increased. The result of the final test is shown in Table 1.

Table 1. Percentage of injury by atmospheric drought to different varieties and strains of sorghum treated in the morning and in the afternoon at three different stages of growth. (Treated for five hours at 125° F. with relative humidity 25-32 per cent)

Days after planting		9-10 days						18-19 days						25-26 days					
Time of treatment	Varieties and strains	1st test Pot No.			2nd test Pot No.			1st test Pot No.			2nd test Pot No.			1st test Pot No.			2nd test Pot No.		
		1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
8:30 a.m. to 1:30 p.m.	Blackhull Kafir	5	5	5	20	15	10	80	90	100	90	90	85	80	90	90	80	60	75
	Dwarf Yellow milo	20	20	20	25	25	30	90	95	100	95	100	100	90	90,	90	90	90	95
	Kaoliang No. 8	20	20	20	15	20	10	100	100	-	90	100	100	100	100	-	100	100	-
	Kaoliang No. 11	20	20	50	50	65	70	100	100	100	100	100	100	100	100	95	100	95	100
	Kaoliang No. 18	20	15	15	75	50	-	100	100	-	100	100	100	100	100	100	100	100	-
	Kaoliang No. 19	10	25	25	30	30	35	95	100	-	95	100	100	100	100	-	100	100	-
	Kaoliang No. 21	20	25	25	85	95	80	100	95	95	100	100	100	100	100	100	95	100	-
	Kaoliang No. 25	30	30	50	85	80	80	95	100	100	100	100	100	100	100	100	95	100	100
2 to 7 p.m.	Blackhull kafir	2	2	2	2	2	2	15	15	25	30	15	15	75	65	65	50	20	40
	Dwarf Yellow milo	20	15	15	15	10	10	70	65	80	55	70	70	90	90	65	55	60	45
	Kaoliang No. 8	10	10	10	10	15	15	90	95	-	100	85	80	75	85	-	75	85	-
	Kaoliang No. 11	25	25	15	15	15	30	65	75	75	90	80	75	65	75	70	60	65	70
	Kaoliang No. 18	20	20	15	20	-	-	100	95	95	100	95	-	85	90	-	100	80	[illegible]
	Kaoliang No. 19	10	10	15	2	5	2	100	95	-	100	100	-	100	100	95	90	-	-
	Kaoliang No. 21	25	25	20	15	10	-	90	90	95	95	95	90	85	90	90	75	85	75
	Kaoliang No. 25	20	25	20	25	25	20	95	90	95	90	90	80	90	80	90	80	75	70

Some pots of Kaoliang Nos. 8, 18, 19 and 21 were missed due to poor germination or to diseases.

Table 2. Analysis of variance of percentage of injury by atmospheric drought to different varieties or strains of sorghum treated in the morning and in the afternoon at three different stages of growth.

Sources of variation	Degrees of freedom	Sum of squares	Mean squares	F Values	One per cent F.
Total	264	334,996.26			
Ages	2	232,520.54	116,260.27	1075.98	4.71
Times	1	24,722.94	24,722.94	228.81	6.76
Ages x times	2	1,148.29	574.14	5.31	4.71
Varieties	7	30,516.84	4,359.55	40.35	2.73
Varieties x ages	14	7,661.75	547.27	5.06	2.17
Varieties x times	7	4,513.36	644.77	5.97	2.73
Varieties x ages x times	14	10,089.70	720.69	6.67	2.17
Tests	1	484.52	484.52	4.47	6.76
Error	216	23,338.32	108.05		

By analysis of variance, it is shown in Table 2 that the variability due to varieties and the interactions of varieties x ages, varieties x times, and varieties x ages x times are greater than that due to error. Therefore the varieties were significantly different in average air drought resistance and some varieties reacted in different manner than others at certain age and in certain time of treatment. These will be brought out in Tables 3 and 4.

Table 3. Average percentage of injury by atmospheric drought to different varieties and strains of sorghum at different stages of growth.

Varieties and strains	9-10 days			18-19 days			25-26 days			General average
	A.M.	P.M.	Ave.	A.M.	P.M.	Ave.	A.M.	P.M.	Ave.	
Blackhull kafir	10	2	6	89	19	54	79	53	65	42
Dwarf Yellow milo	23	14	18	97	68	82	91	67	79	60
Kaoliang No. 8	17	12	14	98	90	94	100	80	90	66
Kaoliang No. 11	46	21	33	100	77	88	98	67	82	68
Kaoliang No. 18	28	19	23	100	97	98	100	89	94	72
Kaoliang No. 19	27	7	17	98	99	98	100	96	98	71
Kaoliang No. 21	55	19	37	98	92	95	99	83	91	74
Kaoliang No. 25	59	22	40	99	90	94	99	81	90	75

Table 4. Average percentage of injury by atmospheric drought to different varieties and strains of sorghum in the morning treatment and in the afternoon treatment.

Varieties and strains	Treated in the morning				Treated in the afternoon				General average
	9-10 days	18-19 days	25-26 days	Ave.	9-10 days	18-19 days	25-26 days	Ave.	
Blackhull kafir	10	89	79	59	2	19	53	25	42
Dwarf Yellow milo	23	97	91	70	14	68	67	50	60
Kaoliang No. 8	17	98	100	72	12	90	80	61	66
Kaoliang No. 11	46	100	98	81	21	77	67	55	68
Kaoliang No. 18	28	100	100	76	19	97	89	68	72
Kaoliang No. 19	27	98	100	75	7	99	96	67	71
Kaoliang No. 21	55	98	99	84	19	92	83	65	74
Kaoliang No. 25	59	99	99	86	22	90	81	64	75

The averages of different stages of growth give indication that the Blackhull kafir was the best in all the stages. At the youngest stage Kaoliang No. 8, No. 19, Dwarf Yellow milo and Kaoliang 19 were the second, while Kaoliang No. 11, No. 21 and No. 25 were the least resistant ones. However, at the stages 18-19 days and 25-26 days after planting Dwarf Yellow milo and Kaoliang No. 11 ranked next to Blackhull kafir, and all the other strains of Kaoliang were significantly lower in resistance. The difference between Blackhull kafir and others was less at the most resistant stage (9-10 days after planting) than at the susceptible stages, while the difference among milo and strains of Kaoliang were just reverse; i. e., greater at the resistant stage than at the susceptible stages. This was due to the severe injury to those varieties besides kafir at the older stages of growth.

Kaoliang No. 8, No. 18 and No. 19 showed very high resistance at the youngest stage. This cannot be attributed to their real ability of resistance but rather to their slow germination. The seedlings were so much smaller than the rest that some of them had only one leaf unfolded. It is unfair to compare them with others, therefore these three strains will not be included in later comparisons.

From the average of the morning treatment we found that Blackhull kafir led in resistance. Dwarf Yellow milo was the next. Kaoliang No. 11, No. 21 and No. 25 were grouped together as the least resistant ones. Difference in response among varieties and strains was shown in the afternoon treatment. There was no change with Blackhull kafir and Dwarf Yellow milo in regard to their relative order but Kaoliang No. 11 rose to a position very close to the milo with only five per cent difference. Kaoliang No. 21 and No. 25 were injured about the same. Here the differences between Blackhull kafir and others were much less in the morning treatment (11 per cent, 22 per cent, 25 per cent, and 27 per cent comparing with Dwarf Yellow milo, Kaoliang No. 11, No. 21 and No. 25 respectively), but the difference increased greatly in the afternoon treatment (25 per cent, 36 per cent, 40 per cent, and 39 per cent respectively). This suggested that Blackhull kafir had gained its resistance from the effect of the light more than the rest of the varieties; in other words, the response of it to the effect of the light was greater than others.

Varietal difference based on general average showed that Blackhull kafir was the most resistant one in the test.

Its percentage of injury was significantly lower than any other. Dwarf Yellow milo was the second. Kaoliang No. 11 was significantly superior to No. 25 but not so to No. 21, although No. 21, and No. 25 were the most susceptible strains.

The effect of ages of seedling on their ability of resistance to air drought was manifested in the significantly small percentage of injury at the stage of 9-10 days after planting. All varieties showed a significant difference between 9-10 day and 18-19 day seedlings as well as between 9-10 and 25-26 day seedlings. Blackhull kafir showed a significant negative difference between 18-19 and 25-25 day seedlings but the rest showed insignificant positive differences. This gave the suggestion that Blackhull kafir either lost some of its resistance at the 25-26 day stage, or was relatively more hardy than the others at the 18-19 day stage. The gain made by the varieties from 18-19 days to 25-26 days were insignificant.

Time of treatment modified the resistance of all the varieties and strains. All of them became more resistant in the afternoon than in the morning, but some responded much more effectively than others. On the average, the greatest difference was found in Blackhull kafir, where the injury was 34 per cent less in the afternoon than in the morning, while the differences of Dwarf Yellow milo and Kaoliang No. 11, No. 21, and No. 25 ranged from 19 per cent to 26 per cent. Low differences of only 8-9 per cent were exhibited by Kaoliang No. 8, No. 18 and No. 19. For the resistant varieties the differences were lower at the resistant stage and much higher at the susceptible stages, while for susceptible varieties the reverse was true. Blackhull kafir had a difference of 8 per cent at the 9-10 day stage but became as high as 70 per cent at 18-19 day stage. At the last stage the difference lowered down to 26 per cent. This suggested that Blackhull kafir owed its resistance at 18-19 day stage to its ability to respond to the effect of light much greater than at other stages, and that lowered resistance at 25-26 day stage was chiefly due to decreases in its ability of response. The susceptible strains showed higher differences at the resistant stage and much smaller differences at susceptible stage; for instance, Kaoliang No. 21 at 9-10 day stage the difference was 36 per cent, at 18-19 day stage only 6 per cent, and increased to 16 per cent at 25-26 day stage. It seemed that susceptible varieties responded better at youngest stage and the ability of response was gradually lost as the plants grew older and was regained a little at the 25-26 day stage. The range of difference between the morning and the afternoon treatment among those varieties was the greatest at 18-19 days, being from 6 per cent to 70 per cent; much less at 9-10 days, from 5 per cent to 37 per cent; but least at 25-26 days, from 16 per cent to 31 per cent. This was due to the rapidly decreasing response of the resistant variety Blackhull kafir rather than the increasing of the response of those susceptible varieties.

Effect of Soil Moisture on the Resistance of Different Varieties and Strains

Table 5 gives the result of percentage of injury of five varieties. The injury was somewhat more severe to the plants in the soil that contained optimum moisture, but by analysis of variance it was found that the difference was insignificant. However, from observation there was some difference in the after effect which was pronounced in the case of Dwarf Yellow milo. Of six pots treated in the morning all plants in soil of high moisture died before the end of two weeks after treatment while those in optimum moisture recovered and started to grow. Of the afternoon treatment, the injury was less prominent, only two pots of the plants in the high moisture died, but all six pots of the optimum moisture recovered. All other varieties showed the same phenomenon but not to as great an extent as Dwarf Yellow milo. This seemed to suggest that the root systems in the soil of optimum moisture had not been injured as much as those in the soil of high moisture.

Table 5. Percentage of injury by atmospheric drought to different varieties and strains of sorghum in soil nearly saturated with water and soil with optimum moisture during the treatment. (Treated at 125° F. with relative humidity 15-23 per cent.)

Time of treatment	Varieties and strains	First test: High soil moisture, Pot No. 1	2	3	First test: Optimum soil moisture, Pot No. 1	2	3	Second test: High soil moisture, Pot No. 1	2	3	Second test: Optimum soil moisture, Pot No. 1	2	3
8:30 a.m. to 1:30 p.m.	Blackhull kafir	60	65	60	80	80	80	90	85	80	90	85	85
	Dwarf Yellow milo	65	75	75	80	70	90	90	90	90	95	95	95
	Kaoliang No. 11	100	95	95	100	100	100	95	95	95	100	100	100
	Kaoliang No. 21	100	100	100	100	100	100	95	95	100	100	100	100
	Kaoliang No. 25	95	100	100	100	100	100	95	95	95	95	95	95
2 to 7 p.m.	Blackhull kafir	20	20	20	35	30	30	10	15	10	15	20	10
	Dwarf Yellow milo	55	55	55	60	60	50	40	30	25	40	30	40
	Kaoliang No. 11	75	80	80	90	90	85	50	55	75	70	70	85
	Kaoliang No. 21	75	85	100	85	85	90	65	65	80	75	65	65
	Kaoliang No. 25	95	90	85	85	85	90	60	60	85	70	70	75

During morning treatment of the second test the temperature rose to 135° F. at the end of the first half hour but lowered gradually to 125° F. at the end of second hour.

Table 6. Analysis of variance of percentage of injury by atmospheric drought to different varieties and strains of sorghum in soil nearly saturated with water and soil with optimum moisture during the treatment.

Sources of variation	Degrees of freedom	Sum of squares	Mean squares	F Values	One per cent F.
Total	119	96,708.125			
Varieties	4	31,961.250	7,990.312	33.00	3.51
Moisture	1	676.875	676.875	2.79	6.90
Time	1	31,525.208	31,525.208	130.21	6.90
Interactions					
Varieties x moisture	4	405.416	101.416		
Varieties x times	4	6,457.083	1,614.271	6.67	3.51
Times x moisture	1	5.209	5.209		
Varieties x time x moisture	4	656.251	164.063		
Test	1	1,050.208	1,050.208	4.33	6.90
Error	99	23,970.625	242.127		

Effect of Hardening on the Resistance of Different Varieties and Strains

The degree of injury to pretreated and control plants is shown in Table 7. By analysis of variance it is found that there are significant differences between pretreated and control plants. Pretreated plants were highly resistant to the atmospheric drought. The control plants, though not so resistant as the pretreated ones, were hardened by gradual rising of temperature and showed that their ability to withstand air drought increased greatly, if the figures of the last column in Table 9 were compared with the average injury to the plants at 18-19 day stage in Table 3 (for the control plants were 20 days after planting).

Table 7. Percentage of injury by atmospheric drought to pretreated and control plants of different varieties and strains of sorghum treated at a gradually rising temperature in the morning and the afternoon. (Treated at 125° F. with relative humidity 33-35 per cent)

Time* of treatment	Varieties and strains	Pretreated plants Pot No. 1	2	3	4	5	6	Control plants Pot No. 1	2	3	4	5	6
8:30 a.m. to 4:45 p.m.	Blackhull kafir	2	5	5	5	2	5	10	10	10	10	10	10
	Dwarf Yellow milo	10	15	15	15	15	10	20	15	25	20	15	30
	Kaoliang No. 11	35	35	35	35	20	25	55	60	65	75	60	75
	Kaoliang No. 21	10	10	15	15	15	15	60	45	60	45	45	50
	Kaoliang No. 25	30	25	30	20	30	20	60	55	75	60	60	70
11:45 to 5 p.m.**	Blackhull kafir	5	5	2	2	2	2	5	5	5	5	5	5
	Dwarf Yellow milo	20	20	30	20	25	20	55	50	55	60	60	65
	Kaoliang No. 11	40	45	35	35	35	40	65	60	70	60	60	70
	Kaoliang No. 21	35	35	40	50	35	30	85	65	70	70	55	55
	Kaoliang No. 25	60	65	45	55	60	60	80	80	75	70	65	80

* The time includes the interval that the temperature rose from 103° F. and 102.5° F. to 125° F. It took three hours and fifteen minutes in the morning treatment and one hour and forty-five minutes in the afternoon treatment.

** During the afternoon treatment the temperature rose from 125° F. at the end of the fourth hour gradually to 130° F. at the end of the fifth hour.

Table 8. Analysis of variance of percentage of injury by atmospheric drought to pretreated and control plants of different varieties and strains of sorghum treated at a gradually rising temperature in the morning and the afternoon.

Sources of variation	Degrees of freedom	Sum of squares	Mean squares	F Values	One per cent F.
Total	119	71,128.925			
Varieties	4	38,019.467	9,504.867	293.03	3.51
Treatments	1	16,170.408	16,170.408	498.03	6.90
Times	1	5,057.008	5,057.008	155.72	6.90
Interactions					
Varieties x treatment	4	3,239.133	809.783	24.94	3.51
Varieties x times	4	3,431.367	857.842	26.42	3.51
Treatments x times	1	52.009	52.009	1.61	6.90
Varieties x treatment x times	4	1,914.700	478.675	14.71	3.51
Error	100	3,246.833	32.468		

From Table 9 it will be noted that Blackhull kafir showed no significant difference between pretreated and control either in the morning or in the afternoon treatments, but all the others did show a difference. Greater differences were observed among strains of Kaoliang indicating that they had acquired more resistance by pretreatment than had Blackhull kafir and Dwarf Yellow milo. Kaoliang No. 21 was a susceptible strain in all the previous experiments but was quite resistant in this test. It equaled Dwarf Yellow milo in the morning but was significantly less resistant in the afternoon. Kaoliang No. 11 in other tests has been much better than No. 25, but was not very different in the morning test of this experiment. This indicated that there was a varietal difference in response to the pretreatment.

With the exception of Blackhull kafir, the injury to the other sorghums including Dwarf Yellow milo and all strains of Kaoliang was greater in the afternoon than in the morning. This was neither due to the loss of resistance, for the control also showed the increase in injury, nor to the change of the response by the treated plants to the effect of sunlight for Blackhull kafir still showed the same effect of afternoon treatment as in previous experi-

Table 9. Average percentage of injury by atmospheric drought to pretreated and control plants of different varieties and strains of sorghum treated at a gradually rising temperature in the morning and the afternoon.

Varieties and strains	Pretreated plants			Control plants		
	A.M.	P.M.	Ave.	A.M.	P.M.	Ave.
Blackhull kafir	4	3	3	10	5	7
Dwarf Yellow milo	13	26	19	21	57	39
Kaoliang No. 11	31	38	34	65	64	64
Kaoliang No. 21	13	37	25	51	67	59
Kaoliang No. 25	26	58	42	63	75	69

ments. It was probably due to the discrepancy of temperature during the afternoon treatment. It rose from 102.5° F. to 125° F. in an interval one and one-half an hour shorter than in the morning and it gradually rose from 125° F. to 130° F. during the last hour of treatment. The more rapid rise of temperature at the beginning and the higher temperature during the last hour of the afternoon test probably both contribute to the greater injury in the afternoon compared with the forenoon treatment.

Another fact that was interesting has been observed. The pretreated plants kept on growing after the treatment, while the growth of control plants was retarded about 10 days.

Injury Caused by Soil Moisture Deficiency

Two weeks after the pots had been set up, the sign of water deficiency began to be manifest. The lowest leaf first discolored, turning into yellow or pinkish, and then desiccated. Discoloration and desiccation started from the tip and margin of the leaf blade and extended downward to the sheath. It proceeded from the lowest leaf up to the top ones. When two or three of the basal leaves had desiccated those upper leaves began to fold up and the rate of desiccation decreased. When desiccation reached to the two uppermost leaves it seemed to stand still for several days. These leaves were not discolored and desiccated gradually as other leaves were, but they desiccated rapidly within one or two days without discoloration. The speed of desiccation of course varied with the environmental conditions and varieties, but the general process was all the same.

Dwarf Yellow milo wasthe first one that showed the sign of soil moisture deficiency. It folded its leaves earlier than any others. Yet it held out longer than the rest.

Difference Among Varieties and Strains in Resistance to Soil Drought

The average of the injury caused by soil drought in Table 10 shows that there were differences in resistance among the varieties and strains. However, analysis of variance shows that the variability was fairly but not highly significant. Also, as the experiment had not been carried out extensively enough to warrant a conclusive result, it only gave some indication that Dwarf Yellow milo seemed to be more resistant to soil drought than any other and Kaoliang No. 21, Blackhull kafir and Kaoliang No. 11 were the next while Kaoliang No. 25 was the most susceptible.

Table 10. Percentage of injury to sorghum varieties and strains subjected to soil moisture deficiency.

Varieties and strains	Pot No. 1	2	3	4	Average
Blackhull kafir	40	95	85	95	79
Dwarf Yellow milo	40	40	65	50	49
Kaoliang No. 11	90	90	55	90	81
Kaoliang No. 21	70	85	70	90	77
Kaoliang No. 25	95	90	95	95	94

Table 11. Analysis of variance of percentage of injury to sorghum varieties and strains subjected to soil moisture deficiency.

Sources of variation	Degrees of freedom	Sum of squares	Mean square	F Value	5 Per cent F.	1 Per cent F.
Total	19	8230				
Varieties	4	4380	1095.00	4.27	3.06	4.89
Error	15	3850	256.67			

The result does not agree with those obtained from heat chamber treatment. It suggests that a variety resistant to air drought is not necessarily resistant to soil drought. It will be discussed in the following paragraphs.

DISCUSSION

The injury due to either form of drought is the desiccation of cells. This may not be the direct cause but it is the primary step leading to the course of destruction. Therefore any means that prevent the desiccation of the cell during drought will enable the plant to withstand drought well. Numerous studies have been done on this point. It is to some of the morphological and physiological characters that the capacity of plants to endure drought has been attributed. It is logical to think that these characters must work together or that by their interaction plants show the ability of resistance. We cannot say which one is most important, but certain factors may be predominant under certain conditions.

Under the condition of atmospheric drought the temperature is so high and relative humidity so low that an exceedingly high transpiration is induced. Plants that are capable of withstanding such a condition must have a large root system to absorb sufficient water to replace the amount lost in transpiration and an efficient conducting system to transfer water fast enough to meet the rapid loss. On the other hand the leaves should reduce the rate of transpiration by closing stomata or possibly very slightly by raising the osmotic pressure of the cell sap through the increase of concentration, or by augmenting imbibitional pressure through the increase of hydrohylic colloids.

In fact at high temperatures, especially the plant grown in the pot, the temperature of the soil may become so high that the function of the roots is severely retarded or the roots may even be killed. Therefore it is not only the total number and length of the roots that determine the resistance of plants to drought, but the response of the roots to the effect of high temperature should be considered too. In this experiment the roots of Kaoliang seem to be much more susceptible to heat than kafir and milo.

It has been found when the temperature is extremely high or when plants are severely wilted the stomata open widely and lose the ability to close. Thus only the number of stomata in a unit of the area of the leaf and the total leaf surface are the determining factors of water loss if all other characters are similar.

In the present investigation, four kinds of difference in resistance; i.e., resistance due to varieties, to ages, to time of treatment, and to hardening are observed. Do they owe their resistance to some causes in common or not? This is a question worth further investigation. So far as one can infer, it appears that they are not necessarily alike in causes.

Varietal difference may be explained on the basis of different morphological and physiological factors, but what makes the younger plants of the same variety much more resistant than the older plants? Probably this is a good illustration of Iljin's finding as shown by Maximov. The experimental evidence secured by him shows that desiccation is not injurious to protoplasm, but the mechanical rupture of the protoplasm during shrinkage due to rapid loss of water in the vacuole kills the cell. If protoplasm is separated from the cell wall gradually, such as takes place during plasmolysis, the cell would be saved. According to him the protoplasm of every plant cell can endure complete desiccation if the rupture of it could be prevented. Absence of a vacuole, or the vacuoles filled with various substances as starch, fats and proteins are the best means of prevention of rupture. In young seedlings most of the cells have not attained their full development so their vacuoles are small; thus on desiccation no rupture will result and so the plants are more resistant. Furthermore, the presence of a large amount of protoplasm will hold water in a bound state which adds much to the resistant ability of the plant. Another possible morphological character may be that the stomata on those young leaves have not fully developed so the transpiration is less.

The difference between the morning treated plants and afternoon treated plants is entirely due to physiological factors. It is well known that leaves of the plant under the influence of sunlight exhibit a rhythmic change of the water content and dry matter. According to Miller's investigation in 1917 in milo leaves the water content falls gradually from seven o'clock in the morning to a minimum which is reached from one to three o'clock in the afternoon, while dry matter increases progressively from seven o'clock in the morning to a maximum which is reached between three and five o'clock in the afternoon. From this we may imagine the change taking place in the cells. Naturally the concentration of the cell sap is higher in the afternoon than in the morning. The question is whether there is any change in colloidal content. Of this we cannot be assured. Anyhow, the osmotic pressure of the cell sap is increased, which possibly lowers the rate of transpiration slightly and favors the plant to stand desiccation. Most of the materials accumulate in the cells of leaves in the day time and are transferred or assimilated during the night so the resistance is lowered again by the next morning.

The effect of hardening on the cells by subjecting the plants to wilting has been studied by Levett and Scarth (1936). Their results indicate that both the osmotic pressure of the cell sap and the permeability of the protoplasmic membrane increased. Also the experimental evidence of Vassiliev and Vassiliev (1936) shows that the amount of sucrose and hemicellulose increases in the cell. What happens to the plants hardened at a moderately high temperature or at gradually rising temperatures, we do not know. It may not be far from those studied, but the colloidal substance in the cell is believed to be affected either qualitatively or quantitatively. Therefore hardened plants acquire their resistance from physiological changes in the cells. However, according to Maximov, Tumanov 1937, in that plant hardened by single severe wilting the subsequent growth was retarded. This was true in the plants hardened by gradually increasing temperature but apparently not in those hardened by moderately high temperature and treated at gradually rising high temperature. This may lead us to think that such a hardening as the latter is more desirable and that there must be some difference in the changes. Also the factors responsible for the resistance by hardening may in certain respects differ from those brought about by light. This is shown by the different response among varieties and the higher degree of resistance manifested by all the varieties after hardening. How long will the effect of hardening last is an interesting question. The result of Tumanov's experiments seems to indicate that the effect will continue for the rest of the life of the plant. Vassiliev and Vassiliev also suggest that the change of the cell content seemed to have become fixed. However, more investigation is required before we can be sure.

Under the condition of soil drought, the plant is subjected only to the stress of the gradual diminishing of water and finally, perhaps, to the entire depletion of it. Here the temperature is not necessarily extremely high and the rate of transpiration not so rapid as in air drought. The only analogy of this condition with that in the heat chambers was the insufficiency of water in relation to the demand of the plant. Because under this condition the water in the soil became really scarce so the plant could not absorb enough to maintain normal growth, and under the conditions of the heat chamber the absorbing power of roots might be interferred with or the water carrying capacity of the plant might be so limited that it could not get a sufficient quantity for transpiration. Under such a stress the plant with a large root system and small transpiring surface would surely be benefited as brought out by Miller (1931). Such a plant would wilt much later. However, as soon as the permanent wilting point was reached, all the available soil moisture having been used up, the role played by the roots was negligible. At the same time the plant had been gradually hardened by the progressive drying. Now any means, morphological or physiological, that minimized further loss of water from the cells would determine the endurance of the plant.

In heat chamber tests, Blackhull kafir was superior to Dwarf Yellow milo in every case, but the order was reversed in the soil moisture deficiency test. Whether the effect of gradual drying had induced another type of resistance, we did not know, but judging from the relative rank of three strains of Kaoliang, it indicated the effect of drying had produced some kind of hardening. Therefore for the cause of such a reverse we should resort to the morphological difference that gives milo special adaptation to such a condition. The studies made by Miller (1931) on the root system studied in 1916 and stomata number studied in 1928 of Blackhull kafir and Dwarf Yellow milo revealed that on the average kafir had two more roots of secondary order on each inch of the root of first order and that kafir had a total number of 146.7 thousands of stomata per square inch of leaf surface, while milo had 150.4 thousands. This explained a part of why Dwarf Yellow milo was less resistant to air drought and wilted earlier in the soil moisture deficiency test. When wilting set in Dwarf Yellow milo folded up its leaves tightly and so reduced the transpiration from the stomata on the upper leaf surface. Blackhull kafir did the same two or three days later. Now, if all the other things were equal between these two varieties, the major factor that governed the further loss of water from the leaf would be the number of stomata on the lower leaf surface. Miller's data showed that Blackhull kafir on the average had 96.5 thousands per square inch of lower leaf surface while Dwarf Yellow milo on the average had only 86.7 thousands. This factor may favor kafir in heat chamber tests for leaves never fold up therein, but it may be significantly in favor of milo in the case of soil drought as soon as wilting begins. The total leaf surface of kafir is much larger than milo when the plants approach mature size, but at the seedling stage the total leaf area between these two varieties does not show much difference, therefore the ratio of stomata on lower to upper leaf surface serves as a possible explanation for the superiority of Dwarf Yellow milo in this experiment.

Among the three strains of Kaoliang the relative rank of the strains is in the same order as in the hardening experiment. From this we may infer that plants do harden by wilting and that Kaoliang No. 21 responds to the hardening process better than the other two strains as it did in hardening for atmospheric drought.

From the above discussion it is clear that both morphological and physiological characters are responsible for the drought resistance of plants. The environmental conditions and the way that the plants respond determine the value of these characters. A character that is entirely functionless under one set of conditions may be of vital importance under another set of conditions, or a leading factor at one stage of plant growth may be negligible at another stage. This also may explain the contradictory results of investigations made in the past.

In the present experiments only the seedlings were studied. When the plants grew to their full size, there was a great change in their morphological characters; for instance, kafir had more leaves than the others while the size of the leaf of fully grown Kaoliang was usually smaller than kafir and milo. These morphological changes may have caused greatly different responses to either form of drought. Therefore it appeaed that treating sorghum seedlings in a heat chamber was advisable for a test of their physiological resistance rather than their morphological resistance. Furthermore in the case of the soil moisture deficiency, plants were more or less hardened. As to the results brought out by those strains of Kaoliang, the respective order of resistance among the strains was close to that of plants treated in gradually rising temperature. This indicated that in treatment for soil drought resistance a satisfactory result could be obtained by using gradually rising temperature provided no disturbing factor was present as in the case between kafir and milo.

SUMMARY

The ability of Blackhull kafir, Dwarf Yellow milo and six strains of Kaoliang grown in pots in the greenhouse to withstand atmospheric drought was tested at three stages of growth in the morning and in the afternoon by means of a heat chamber where the temperature was kept at about 125° F. with a relative humidity varying from 20-33 per cent.

The results showed that all the varieties and strains were more resistant to air drought at the stage 9-10 days after planting than when the plants had grown 18-19 days and 25-26 days after planting.

Plants in the morning were more susceptible to air drought than in the afternoon.

Blackhull kafir was the most resistant in all the cases and Dwarf Yellow milo was second. Three strains of Kaoliang due to slow germination disturbed the result especially at the 9-10 day stage so they were not included in the comparison. Other three strains showed that they were more susceptible than Dwarf Yellow milo to air drought. Among the three Kaoliangs, No. 11 was somewhat superior to the other two, No. 21 and No. 25.

Some of the varieties or strains responded differently in the morning and afternoon treatment and at the different stages of growth.

Difference of moisture in soil nearly saturated and optimum produced no significant influence upon the resistance of the plants but there was indication that the after effects of the air drought on the plants in optimum moisture were not so severe as on the plants in the nearly saturated soil.

Hardening the plants of 19 days after planting by a pretreatment at temperature 110° F. for four hours or by gradually raising the temperature from 103° F. or 102.5° F. to 125° F. within an interval of three or two hours increased the resistance of the plant greatly.

Greater response to hardening was manifested by Kaoliang No. 21 than by Kaoliang No. 11 or No. 25.

By subjecting the plants to soil moisture deficiency we found some indication that Blackhull kafir was not so resistant as Dwarf Yellow milo and Kaoliang No. 21 was more resistant than other strains of Kaoliang. This seemed to suggest a variety resistant to air drought was not necessarily resistant to soil drought and vice versa. However, further test is required before we can assure this.

A discussion on the ability of plants to resist air drought and soil drought was made to show the importance of both morphological and physiological characters of the plant in relation to environmental conditions, and the response of plants under those conditions.

ACKNOWLEDGMENT

The advice and helpful suggestions of Dr. H. H. Laude, under whose direction these studies were made, are sincerely appreciated. Thanks are due to the Department of Agronomy of Kansas State College and the Yenching University and Agricultural Experiment Station, Peiping, China for the seeds used in the experiments.

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