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Mechanisms of Heat and Drought Resistance in Grain Sorghum and Methods of Measurement

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16. MECHANISMS OF HEAT AND DROUGHT RESISTANCE IN GRAIN SORGHUM AND METHODS OF MEASUREMENT

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I. Introduction

The majority of the world's sorghum crop is grown under unirrigated conditions and there is little doubt that this will continue for many years to come. Therefore, efforts will continue to be directed toward gaining an understanding of the mechanisms which impart drought resistance to this crop and to utilization of this knowledge in breeding programs.

Progress has been made in the past in breeding for drought resistance by empirical methods and more will be made in the future. However, it is believed that greater progress can be made if we have a good knowledge of the internal water status and physiological responses of the crop when grown under many different environments, all having in common a "drought" condition sometime during the growth cycle.

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The term drought resistance is often rather vague in meaning. In reference to our subject grain sorghum, there is little doubt that the most common usage is simply that sorghum producing the greatest grain yield in a specific locality with limited soil moisture. The problem we are confronted with is defining the contributing factors that enabled the more drought resistant to produce more grain.

In the case of wheat, Asana (1961) found that the effect of drought was greatest in reduced grain number and 1,000 grain weight, whereas, under adequate soil moisture, ear number had the most dominant effect on yield. He further reported that ear yellowing of a more drought resistant variety was slower than it was with a less resistant variety. It was indicated that decreased photosynthesis due to chloroplast or chlorophyll instability contributed to the decreased yield of the less drought resistant. A question pending is whether water potentials of the wheat leaves were the same at the time differences in yellowing were observed. Would chloroplast degradation occur at different water deficits or did the more drought susceptible simply reach a critical deficit sooner than the more drought resistant? This is a rather simplified question, but when studying the great diversity of plant types, particularly as found in sorghums, it seems that defining water potentials is absolutely necessary if we are to understand their drought responses.

Levitt (1956, 1958, 1964) has for many years recognized that total drought resistance of plants in any environment is due to either avoidance or tolerance mechanisms. Accordingly, the terminology of this paper will generally follow that of Levitt *et al.* (1960) for consistency and clarity. Drought avoidance (evasion) includes any mechanism which keeps the tissue water potential above that which would cause cellular injury. Avoidance is relative, and it is difficult to place a value on it, but it could be said that it is the number of bars water potential maintained in the field above that which would cause 50% killing of the cells. It is thus assumed that the greater this value, the less are the direct detrimental effects of the existing reduced water potential on cellular activity. Avoidance mechanisms include the ability to keep the water potential high by absorption of water and conduction to the shoot or ability to reduce water loss, e.g., by stomatal closure. Completion of the life cycle or some critical stage in the cycle before the damaging drought occurs would also be an avoidance mechanism.

Drought tolerance (desiccation tolerance) is defined as the equilibrium relative humidity (or water potential) which causes 50% killing of the cells. That is, at a slightly higher water potential the cells will survive

2

or function metabolically although the tissues are desiccated. It is here assumed that the greater the desiccation tolerance, the less the direct effects of reduced water potential will be on metabolic activity and cellular injury, other than that resulting in killing of the cells. I will also refer to water potentials resulting in visible tissue damage as the critical water potential.

The relationship between relative humidity and water potential is as follows:

$$\text{relative humidity} = p/p_o$$

where p is the vapor pressure of the water in the air at a given temperature and p_o is the vapor pressure when it is saturated at the same temperature, and

$$\text{water potential} = RT/V \text{ in } p/p_o$$

where R is the gas constant, T the Kelvin temperature, and V the partial molal volume of water. Water potential is negative since it is referenced against pure water at the same temperature.

Equivalent terminology of avoidance and tolerance is used for heat resistance. Any means for cooling the plant, for example by transpiration or reflection, may enable it to avoid heat injury, and its heat resistance would then be due to heat avoidance. Heat tolerance, on the other hand, is the ability to live and function metabolically when the plant is actually at the high temperature.

Total drought and heat resistance is the result of many complex and interacting tolerance and avoidance mechanisms. The mechanisms in sorghum are just as complex as they are in other crops. It is because of the complexity of the problem that it is most desirable to systematically evaluate the heat and drought resistance characteristics of the crop first in terms of avoidance and tolerance, then follow with more specific characterisation of the type of avoidance or tolerance mechanisms.

New techniques or modifications of older techniques and new instrumentation have been developed in recent years which facilitate measuring plant water stress (Sullivan, 1971). The pressure bomb (Scholander *et al.*, 1965) is useful for field and greenhouse measurements of sorghum leaf water potentials. It is relatively inexpensive, simple to construct and portable. When standardized with thermocouple psychrometers, perhaps the most accurate method of measuring water potentials, the pressure bomb has given us accurate and convenient measurements of water potentials to about −35 bars. We have had difficulty with sorghum leaf tear and crushing at higher pressures, although this was mini-

3

mized by use of a molded silicone stopper for holding the leaf strip in the bomb (Blum *et al.*, 1971b).

II. Critical Water Potentials

Using the pressure bomb and thermocouple psychrometers (Spanner, 1951; Box, 1965a, b) we have found that commercial field grown sorghums in Nebraska generally survive at leaf water potentials ranging from −26 to −35 bars during the maximum stress period of the day, but growth nearly, if not entirely, ceases during this period. Measure of field water potentials, when related to visible estimates of growth and development, are thus also a measure of critical water potentials.

Varietal differences in critical water potentials were evident with plants grown in sand-nutrient cultures in large tanks, 3 × 10 × 2 feet deep, in the greenhouse. Two hybrids, RS-626 (U.S.) and CSH-1 (India) were grown in mixed culture in one of the tanks. Two rows were planted 46 cm apart and 15 cm between plants, with a total of 36 plants. They were planted so that every other plant was the same hybrid. The purpose of this mixed planting was to intermix the root systems so that root moisture availability would be the same for the two hybrids. At approximately six weeks plant age any excess nutrient in the bottom of the tank was drained and they were not watered again for about three weeks. Leaf water potentials were periodically measured on ten plants of each hybrid. At maximum stress the average water potential of the second leaf from the top of all plants of both hybrids was −33 bars. When rewatered all of the CSH-1 plants recovered but none of the RS-626 plants recovered. Desiccation tolerance of RS-626 was thus much lower than that of CSH-1. At the time of the drought injury RS-626 was about 30% pollinated and CSH-1 was in the early boot stage. The difference in stage of development may at least partially account for failure of RS-626 to survive the desiccation stress. An experiment shown later will support this view.

There was no evidence of differences in avoidance mechanisms of the two hybrids when the root systems were placed under identical conditions. The difference was almost entirely one of tolerance. Results of heat tolerance tests also showed that CSH-1 had higher heat tolerance than RS-626. After one hour at 49°C CSH-1 had 76% injury and RS-626 had 93.5% injury.

.4

III. Measuring Heat and Drought Tolerance

The above mentioned relation between heat and drought tolerance brings up a point to be discussed. It is known that there is often positive correlation between desiccation tolerance and heat tolerance (Levitt, 1956, 1958; Sullivan and Blum, 1970). A simple test has been employed in our laboratory to measure both heat and drought tolerance. It uses leaf discs and an electrical conductivity method to measure both. The method was modified from Dexter *et al.* (1932) by Sullivan and Kinbacher *et al.* (1967) and Sullivan *et al.* (1968).

Some minor modifications have been made in the procedure since we first described the method, and the procedure of the heat test as we now normally use it will be briefly described. The procedure for the desiccation tolerance test is essentially the same as for the heat tolerance test except after the initial wash period the leaf discs are blotted dry and placed in small jars over KCl solutions giving known relative humidities. The discs are allowed to equilibrate with the R. H. of the jars for 48 to 72 hours. When the discs are removed from the jars they are put in test tubes and the remainder of the procedure is the same as for the heat test.

Twenty one cm leaf discs are cut for each test with a cork borer, placed in a test tube, and washed thoroughly with distilled water for about two or three hours with at least four changes of water during this period. This step is important since it washes out the contents of cut cells and other readily diffusible electrolytes. At the end of the wash period the water is drained off, but enough water should remain to keep the discs wet during the heating treatment. The tubes are covered with plastic wrap and stood in a thermostated water bath for one hour at 48°C. A duplicate sample is held as a control at room temperature. After heating, thirty ml of distilled water is added to each test tube and they are held overnight in an incubator at 10°C. The next day (18 to 24 hours) the relative amount of electrolytes diffusing from the tissues is measured with a conductivity bridge and dip cell which fits into the test tubes. Each tube is stirred with the dip cell before the reading is taken. The tubes are placed in a 25°C water bath and allowed to equilibrate with this temperature before the conductivity is measured.

After the first conductivity reading is taken, the tubes are again covered with plastic wrap and the samples completely killed by autoclaving the tubes for 5 to 10 minutes, or placing the tubes in boiling water until the water in the tubes reaches about 90°C. The tubes are

then cooled to 25°C and the conductivity again measured. The first reading is then calculated as a percentage of the second. The injury value calculated from the elevated temperatures is then calculated as a percentage of the increased conductance over the controls. For example: the controls Cl/C2 × 100 = 6.0%, 100% − 6% = 94% uninjured; and at 48°C, Cl/C2 × 100 = 60% injury, 100% − 60% = 40% uninjured, 40/94 × 100 = 42.6% uninjured or 57.4% injury, where injury is arbitrarily taken as proportional to the percentage of the conductivity calculated, and Cl is the conductivity before autoclaving and C2 is the conductivity after autoclaving. This calculation allows for injury to the controls by the cutting and handling process and shows only the injury caused by the increased temperatures. The percent injury calculated by this test closely approximated the actual tissue killing observed after treating intact plant in heat chambers or shoots of potted plants submerged in water baths at the same temperature as the discs were heated (Sullivan *et al.*, 1968).

It may be necessary to use a series of temperatures for the first few tests made on a particular type of plant material in order to find the

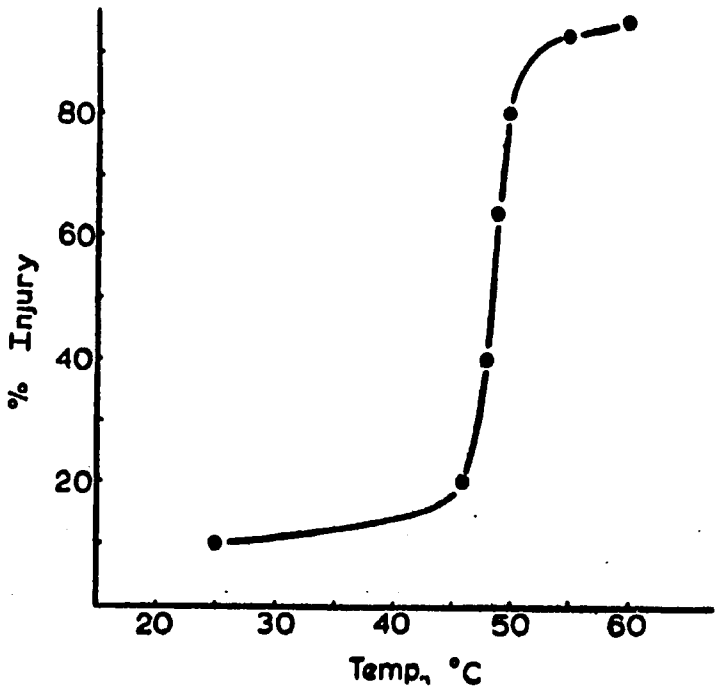

FIG. 16-1. An example of the conductivity method of testing for heat tolerance with leaf discs.

6

temperature that causes about 50% injury. Since the injury versus temperature curve is sigmoid, as shown in Fig. 16-1, the area around the 50% injury point is the most sensitive.

Results from the heat test have been compared to observations on different plant species and varieties with known drought resistance from field experience. Those with greater field drought resistance also had the highest heat tolerance (Sullivan *et al.*, 1968). Others have also found positive correlations between heat and drought resistance (Julander, 1945; Kaloyereas, 1958; Kilen and Andrew, 1969; Williams *et al.*, 1969). We also found good agreement between the heat tolerance of leaf discs and heat stability of the photosynthetic activity of chloroplasts isolated from the same plants (Sullivan and Eastin, 1969). Similarly, the effects of drought stress on photosynthetic rates of leaf segments agreed with heat tolerance tests. The sorghum M35-1 had higher heat tolerance than RS-610 (Sullivan and Yoshikawa, 1969; Sullivan and Eastin, 1969; Sullivan and Blum, 1970), and there was less reduction in the photosynthetic rate of leaf segments of M35-1, even with lower leaf potentials (greater stress), than RS-610 when measured under environmentally controlled conditions (Blum and Sullivan, 1971).

IV. Range of Heat Tolerance in Sorghum

Wide differences in heat and drought tolerances of sorghums have been found. A number of yellow endosperm lines, varieties, and hybrids were field grown in Nebraska under good fertilizer conditions, and tested for heat tolerance by the conductivity method with leaf discs taken from the second expanded leaf from the top of the plant. In this case the discs were heated for one hour at 46, 48, 50, and 52°C. The controls were held at room temperature (near 25°C) as usual. The temperature causing 50% injury was found by interpolation. Table 16-1 shows the results of one of these experiments in which tests were made during July and August. Planting date for these sorghums was May 25. It can be seen from the table that temperature range for 50% injury was from 52.0 to 45°C, a difference of 7°C. Further tests were made during the same months on 56 different sorghums. A total of 242 tests were made including 20 plants per test. Heat tolerance was arbitrarily divided into high (49°C or over), medium (47.0 to 48.9°C) and low (46.9°C or below) temperatures causing 50% injury. Of this group 17 ranked high, 32 medium, and 7 low in heat tolerance (Sullivan and Eastin, 1967).

TABLE 16-1. *Heat Tolerance of Sorghums as Determined by the Conductivity Method with Leaf Discs*[1]

Sampling Date		Sorghum								
		9084*	2140*	9024*	9103*	RS-610	RS-501	Martin	Caprock	9039*
July	11-20	51.4	—	51.6	—	50.9	50.7	—	—	45.0
„	21-31	—	52.0	—	—	50.0	50.4	51.2	46.2	49.5
August	1-10	47.6	46.7	48.5	50.8	—	49.6	46.2	48.3	46.0
„	11-20	50.7	49.8	47.9	47.8	49.2	—	46.3	46.0	46.0
„	21-31	50.5	—	—	50.4	47.4	45.0	49.2	—	—
Mean		50.1	49.5	49.3	49.7	49.4	48.9	48.2	46.8	46.6

[1] Each value is the mean of duplicate samples of 20 plants Each. The values give the temperature, °C, at 50 % injury.

*Yellow endosperm sorghums, courtesy of Paul Nordquist, North Platte, Nebraska.

9084—selection from cross 5728 × Tx yellow, 5825-24.

2140—selection from corss 60665 ms ms, Coes × white Martin-short Kaura.

9024—selection from CK60-short Kaura × CK60-Kurgi.

9103—selection from open pollinated yellow crosses made in 1959.

9039—selection from CK60-Kurgi × Tx yellow 5811-2-1, 5812-1.

Mean heat tolerance values correlated positively with mean air temperature maxima, in the above tests, but relative values between sorghums did not appreciably change. During July the average maximum air temperature was 92°F (33.3°C) and the average temperature causing 50% injury was 49.3°C. In August the average maximum air temperature was 83.3°F (28.6°C) and the average temperature causing 50% injury was 48.2°C. This was not believed to be due to maturity differences in July and August, since it has subsequently been found that heat tolerance generally increases with age and parallels increases in osmotic values (Sullivan *et al.*, 1968a).

V. Correlations in Heat and Drought Tolerance

Generally sorghums with high heat tolerance also have high drought tolerance. This was shown when heat tolerance with leaf discs was compared to drought tolerance which was tested in two different ways. One by desiccation of leaf discs in 93% relative humidity for a constant time, and the other by allowing excised plants to desiccate and periodically measuring the water potential of the leaves as they dried. The water potentials were then compared with visual estimates of 50% leaf injury of the plants after standing their excised leaves in water (Sullivan and Blum, 1970).

This positive correlation between heat and drought tolerance, however, is not always found, and comparisons between species have not always shown that high desiccation tolerance is accompanied by high heat tolerance. Pearl millet, HB-1 and its parent lines, for example, were found to have very high heat tolerance, but desiccation tolerance was relatively low when compared to several sorghums. The same relation was found for corn, although the difference was less (Table 16-2).

TABLE 16-2. *Heat and Drought Tolerance of Sorghum, Pearl Millet and Corn, as Determined by the Electrical Conductivity Method with Leaf Disc**

	Heat Tolerance *(Percent injury)*	Drought Tolerance *(Percent injury)*
Sorghum		
RS-610	53.7 a**	60.1 a**
M35-1	33.2 b	44.0 b
Millet		
HB-1	12.0 c	84.0 c
Tift 23A	13.6 c	80.3 c
Corn		
Hays Golden	25.0 b	72.5 d

* Discs were exposed one hour to 48°C and 48 hours in 96% relative humidity. Values are means of four replications.

** Means not followed by the same letter in a column are significant at the 5% level.

9

A study of stomatal responses showed that the millets closed their stomata at higher water potentials (less stress) than several sorghums. The literature also indicates that corn close their stomata sooner than sorghum under drought stress (Sullivan and Blum, 1970). When stomata close due to drought stress, leaf temperatures are expected to increase. Exposure to higher leaf temperatures is also expected to result in a heat hardening effect. It is, therefore, quite conceivable that corn and pearl millet have been inadvertently selected that can tolerate increased leaf temperatures. Sorghum, with stomata partly open, may maintain enough transpirational cooling to avoid excessively high leaf temperatures. By process of elimination, it can be concluded that the drought resistance of pearl millet is due primarily to other drought avoidance mechanisms. This is in agreement with the conclusions of Fanous (1967). Corn apprently lacks these other avoidance mechanisms, thus lending it more drought susceptible.

It is apparent from these results that the mechanisms responsible for increased heat tolerance in pearl millet and corn are not equivalently increasing desiccation tolerance. This may be analogous to cold hardening which increases drought tolerance (Levitt *et al.*, 1960) but drought hardening fails to increase cold tolerance (Levitt, 1956).

In spite of these disagreements that sometimes occur in correlating heat and desiccation tolerance, it is concluded by the author that heat tolerance tests, which are much easier to perform than desiccation tests, can be used as an initial selection tool for both high heat and high desiccation tolerance within a species. It is necessary to test them independently, however, after selection numbers have been reduced.

VI. Basis for Selection

The decision still remains as to whether high or low tolerance is most desirable for maximum yield in a particular environment subject to drought. We dc not have enough information to make a strong decision at this time. However, on the basis of what is known, perhaps one can make a sound guess. Plants with high drought tolerance are generally associated with decreased growth and development, smaller leaves and cell size, and frequently lower, more stable metabolic activity, etc. Plants that avoid tissue drought most of their life cycle generally have very little ability to tolerate desiccation, therefore, if the condition arises where their avoidance mechanisms are not adequate to keep the tissues at a high water potential, they will greatly suffer and may be severely

10

injured or even succumb to the drought. It, therefore, seems desirable to select plants which are intermediate in both avoidance and tolerance mechanisms. Avoidance mechanisms will keep the plants growing and developing and tolerance mechanisms will enable them to survive if the drought becomes severe.

An example of an intermediate avoidance mechanism may be evident in sorghum stomatal response under drought stress. It was reported by Glover (1959) that sorghum stomata remained partly open even during severe drought. Whereas, the stomata of corn were closed most of the day. Similarly, we found the drought resistant corn Conico from Mexico closed its stomata at water potentials near that of sorghum and it also had high desiccation tolerance (Sullivan and Blum, 1970).

If most corn varieties close their stomata sooner than sorghum, it would be expected that avoidance of transpirational loss of water would be greater in corn than sorghum. However, it would also be expected that increased diffusive resistance to carbon dioxide would be greater in the case of corn and consequently photosynthesis would have a greater decrease. In sorghum, however, the internal diffusive resistances, or so called mesophyll resistance, may also increase with stomata partly open. It was found by Blum *et al.* (1971a) with five sorghum varieties grown in soil in a growth chamber that the stomata of plants submitted to two consecutive soil drying cycles remained partly open during the second cycle and leaf diffusive resistance steadily increased. Leaf water potential also steadily decreased. It was thus concluded that control over transpiration was mostly non-stomatal in the second cycle. It is unknown whether diffusive resistance to carbon dioxide parallels that of water in this case.

The same trend was found in our experiment with the sorghum CSH-1 grown to near maturity in a large sand culture tank in a greenhouse. The conditions of growth were same as that previously described for CSH-1 and RS-626 mixed. The plants received full nutrient with about 10 cm excess standing in the bottom of the tank until the plants were about six weeks of age. The tank was then drained and water withheld until permanent wilting occurred. Full nutrient was then given again for several days. The drought cycle was then repeated. In all, three consecutive droughting and re-watering cycles occurred, as shown in Fig. 16-2. Water potentials were measured with thermocouple psychrometers on discs cut from the second expanded leaf of twenty plants. Diffusive resistance was measured on ten plants with a diffusive resistance meter (Kanemasu *et al.*, 1969) as modified by Lambda Instru-

11

ments, Lincoln, Nebraska. Twenty-four stomatal widths were measured microscopically from plastic impressions of six leaves by the method of Brown and Rosenberg (1969).

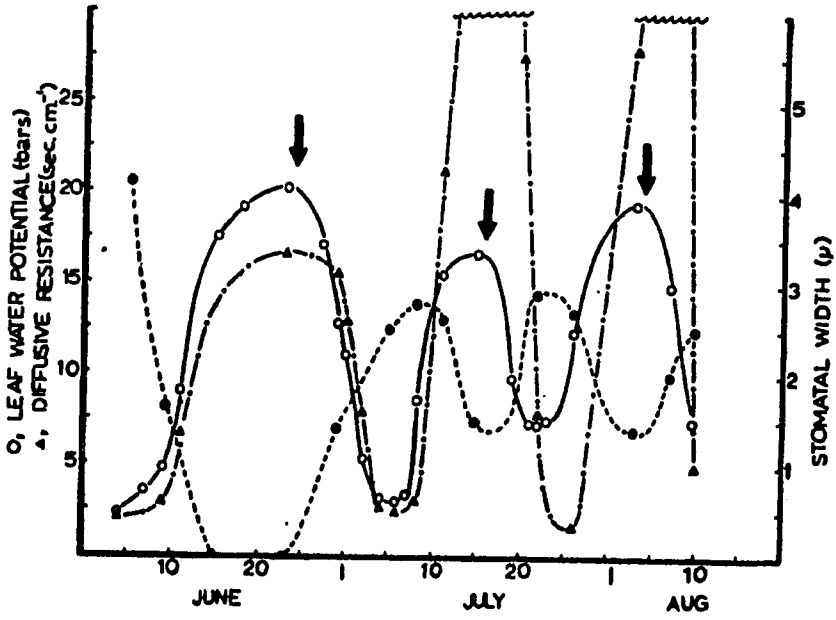

FIG. 16-2. Effects of changing leaf water potentials on stomatal aperture and diffusive resistance during three consecutive drying and rewatering cycles of sorghum CSH-1. Open circles are water potential (o), blackened circles are stomatal aperture (●), and triangles are diffusive resistance (△). The arrows indicate time of rewatering.

As shown (Fig. 16-2) the stomata continued to respond to changes in leaf water potentials, but there was less response on the second and third cycles. There was, however, an increase in leaf diffusive resistance during the latter two drying cycles. During these cycles diffusive resistance exceeded 30 sec cm^{-1}, but stomatal widths remained at about 1.5 microns. The indication was again, as concluded by Blum *et al.* (1971a) that internal resistance becomes progressively greater in controlling transpiration with successive drought cycles.

Drought tolerance may be important in the Great Plains of the U. S. where survival through the drought periods until the next rain falls may mean the difference between some crop produced and complete or almost

12

complete crop failure. In other cases, such as with unirrigated crops of the *rabi* season in India, or other regions which receive little or no additional soil moisture during the entire season, a longer survival after the permanent wilting point may be of no significance, as pointed out by Asana (1965). In this case, varieties that can both tolerate and avoid the drought throughout the season may produce some crop.

Avoidance mechanisms may also be important with sorghums grown in the U. S. Great Plains. This was apparent in an experiment conducted with two U. S. hybrids, RS-610 and Dekalb C-42y, a drought resistant yellow hybrid (Sullivan and Blum, 1970). They were grown in field plots under unirrigated conditions in Nebraska. At about 80 days from planting, soil and leaf water potentials and leaf diffusive resistances were measured. Table 16-3 shows the results of this experiment.

TABLE 16-3. *Soil and Leaf Water Potentials and Leaf Diffusive Resistances of Sorghum Hybrids RS-610 and Dekalb C-42y on August 12-14, 1969 in Unirrigated Field Plots (from Sullivan and Blum, 1970)*

Hybrid	Soil Water Potential Depth, inches (atms.)*	Leaf Water Potential (atms.)**	Leaf Diff. Res. (sec/cm.)***
RS-610	−8.1 − 8.0 − 9.1	−13.0	3.39
C-42y	−9.8 −14.4 −13.6	−14.1	3.94

* Mean values of three samples each from the middle of 4-row, 20 feet length plots and two replications.

** Mean values of two samples of ten leaf discs (1-cm) per sample (10 plants) and four replications. The second fully expanded leaf from the top sampled.

*** Means of ten leaves (10 plants) in each of four replications. The second fully expanded leaf from the top measured.

The hybrid C-42y extracted soil moisture to a much lower water potential than RS-610 in the same period of time, indicating it had a more prolific root system than RS-610. The two hybrids were later grown in sand cultures, and although no measurements were made, visual observations of the roots showed that C-42y had a bigger and more ramified root system than RS-610. Similar results were found by Smith and Maunder

13

(1971) with the same hybrids by use of gypsum resistance blocks buried in the soil of field grown plots. It is questioned, however, whether this kind of avoidance mechanism would be desirable in an area with more limited soil moisture at the beginning of the season, since the crop cannot continue this action indefinitely.

VII. Drought Tolerance and Stage of Development

Susceptibility of leaf tissue to drought induced senescence at different stages of plant development is of interest and needs attention in sorghum breeding. It has been reported that sorghum is most susceptible to low soil moisture conditions during the period of flowering and early grain formation (Salter and Goode, 1967). Water use is also at its peak during this period. One might conclude that transpiration exceeds conduction during this period, tissue water potential falls below the critical level, and drought injury occurs at this stage. Our experiments have given evidence that the critical water potential for leaves is also much higher during the floral development and blooming period than during the vegetative stage, or restated, the desiccation tolerance is less.

Sorghums representing six different genotypes, namely, hegari, durra, dwarf yellow milo, Blackhull kafir, feterita and shallu, were grown two plants per pot in all possible combinations (21) and in four replications. At about 60 days of growth watering was reduced and finally withheld completely. Water potentials were randomly checked with thermocouple psychrometers. When they reached an average of near −25 bars, two more days of drying were permitted and the water potential of the second expanded leaf from the top of each plant was measured with a pressure bomb. The plants were then rewatered and in seven days recovery and injury were visually evaluated. Table 16-4 shows the results of this evaluation. Since the roots of the two plants in each pot mingled almost completely, as later examination showed, one would expect no differences in availability of soil moisture to the two plants. Results of leaf water potentials also showed no significant differences. However, there were significant differences in injury to the plants resulting from the low water potentials. Leaves of those in which the head had emerged from the boot were severely injured in all cases regardless of which plant type they were growing within the pot. It was noticed that the panicle branches and rachis remained green and appeared healthy. If seed was set before the water deficit became too severe,

TABLE 16-4. *Visible Rating for Leaf Injury of Six Drought Stressed Sorghum Genotypes After Seven Days from Rewatering, and Mean Leaf Water Potentials at Maximum Stress**

Sorghum Combination** (2 plants/pot)	Hegari***	Shallu	Durra	Feterita	Milo	Kafir
H-H	3.37					
S-S		1.00				
D-D			4.75			
F-F				3.75		
M-M					1.13	
K-K						2.88
H-S	3.88	1.13				
H-D	3.50		4.75			
H-F	3.00			4.13		
H-M	4.00				1.00	
H-K	3.13					4.63
F-M				3.75	1.00	
F-K				4.00		3.88
S-D		1.25	4.88			
S-F				4.63		
S-M		1.00			0.75	
S-K		1.25				4.13
M-K		1.00			1.00	4.75
D-F			4.88	4.75		
D-M			5.00		1.13	
D-K			4.75			4.00
Means	3.48	1.11	4.79	4.17	1.00	4.30
Leaf Water Potentials Means (bars)	—32.2	—33.2	—31.7	—31.6	—29.3	—28.8

* A rating of 0 equals no injury and 5 equals dead leaves. Values are means of four replications.

** H=Hegari ; S=Shallu ; D=Durra ; F=Feterita ; M=Milo ; and K=Kafir.

*** Stage of development: Hegari, range from milk to hard dough ; Shallu, boot ; Durra, head fully emerged but blasted; Faterita, medium to hard dough ; Milo, late boot ; Kafir, milk to hard dough.

grain filling apparently continued, although no rates were measured. Milo and shallu which were still in the boot stage showed little visible injury from the water deficit. Later when the heads emerged, there was no noticeable injury. Previous result (Sullivan *et al.*, 1971; Blum and Sullivan, 1971) indicated that hegari and durra were the most heat and desiccation tolerant prior to anthesis.

Hultquist (1971) found with sorghum stressed to near −40 bars, at about 10 to 14 days after panicle initiation or near the start to penduncle elongation, that the developing florets were completely killed by the stress. The remainder of the vegetative plant was visibly uninjured and completely recovered from the stress when rewatered. The small panicle prior to floret development was not visibly injured by an equivalent stress. It appears from our data and Hultquist's that susceptibility to drought injury progressively increases from the stage of floret development to anthesis.

VIII. Conclusions

Variability of response to drought and mechanisms of resistance are evident from the few results presented here. It is also evident that there is great deal of further research opportunity for study of the drought resistance of the thousands of sorghum types as exemplified in the world collection. We have only touched on the many aspects of drought resistance, but an attempt has been made to emphasise some basic principles and practical methods of measurement. In order for plant breeders to make selections of many of the traits mentioned, specific measurements and tests must be made. An analogy is not too far from improvements made in nutritional and baking quality of wheat, where several factors were first identified and then combined for maximum benefit. They could not be seen with the eye, and selection pressures were obtained from laboratory tests.

Sorghum drought resistances improvement should make greater progress if first avoidance and tolerance mechanisms are identified with many sorghums grown in different environments. Once this is done, decisions can be made as to the combination of factors most desirable for maximum yield in the average environment of the particular location.

16

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17

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