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DROUGHT AND HEAT RESISTANCE OF SORGHUM AND CORN[1]

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In spite of the vast amount of research on plant drought and heat resistance it still plagues us as one of the major problem areas in agriculture. The problem is simple to solve by timely irrigation, but unfortunately it is neither economically feasible nor physically possible to irrigate all crop land. Therefore, there is still strong interest in understanding and utilizing the mechanisms which impart drought resistance to our crops.

Sometimes confusion has arisen in drought papers because of lack of clarity in the terminology employed. The terminology in this paper will follow that of Levitt et al. (1960). Drought resistance is a total term and will refer to ability to stay alive under unfavorable moisture conditions during some phase of the life cycle and ultimately grow and produce grain, in this case by grain sorghum and corn. Drought resistance includes both avoidance (evasion or escaping) and tolerance mechanisms. The latter is the ability of the cells to survive or function although the tissues are desiccated (desiccation tolerance). Avoidance mechanisms include any means for keeping the tissue moisture level high whether it is by ability to obtain ample water, ability to reduce loss of water, or both. The same terminology is used for heat resistance. For example, cooling by transpiration or having a high albedo may enable the plant to avoid high temperatures. Heat tolerance is the ability to live and function when the tissue is actually at the high temperature.

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Assessing a certain drought resistance trait in a variety by lab-

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oratory or greenhouse tests is not necessarily a measure of total drought resistance under field performance. While the measured trait may be expressed in the field, other factors may take a dominant role which masks the trait. Without an equivalent measurement of the same trait in the field one cannot evaluate the significance of the laboratory test. The significance of the trait may also change according to the pattern of stresses prevailing in the field and the sensitivity of the plant at various stages of growth. It may well be that under certain field conditions a plant should possess one mechanism of resistance in the seedling and another at the reproductive stage, etc.

It also seems very necessary to investigate and establish the pattern, degree and timing of stresses under which the plant is expected to perform before defining the type of resistance one should look for. It would be similar to the case of investigating the prevalence, severity and types of wheat rust races in a region prior to embarking on a breeding program for a rust resistant wheat for that region.

Since total drought resistance is a combination of both avoidance and tolerance mechanisms, it is necessary to measure and evaluate them independently. The development of new techniques and equipment in recent years for measuring plant water stress (Sullivan, 1971) has greatly facilitated these measurements. Portable instruments for measuring water potentials and estimating transpiration rates under field conditions are helping bridge the gap between laboratory, controlled chamber and greenhouse results and field performance.

In general grain sorghum has a reputation for greater drought resistance than corn and it has been known for this trait for many years. Martin (1930) quoted Gates in 1922 as referring to kafir as the "crop camel". This term implies its ability to retain water, and Martin concluded that the greater drought resistance of sorghum was due to its ability to evade severe wilting. This was because sorghum retarded water loss primarily by a heavier waxy cuticle, and more secondary roots implemented greater water absorption. He further concluded that sorghums recovered from drought induced dormancy better than corn because their tissues were never exposed to severe desiccation. The ability of sorghums to tiller and head after moisture again becomes available was also noted as superior to corn.

Our knowledge on the comparative drought and heat resistance of sorghums and corn has progressed some since 1930, but Martin's conclusions are still basically sound.

Transpiration

There is evidence that stomatal control over transpiration differs in sorghum and corn. Glover (1959) using a resistance porometer found that during severe drought the stomata of corn were only slightly open during a short period in early morning and closed for the rest of the day. Whereas, the stomata of sorghum remained slightly open all day even during severe drought. Differences were also found in the recovery. When water was restored after severe drought sorghum stomata recovered quickly to their

normal behavior before the drought. The stomata of corn, on the other hand, failed to ever return to their normal behavior after watering, although the leaves were fully turgid and appeared normal. The stomata of newly developed leaves functioned normally, however.

Pallas and Bertrand (1963) showed that corn stomata close at lower soil moisture tension than sorghum (Figure 1). One corn line,

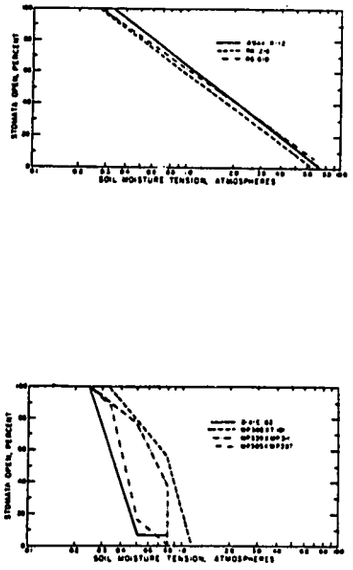

FIGURE 1

Stomatal activity under low CO_2 concentrations in air as related to increasing soil moisture tension—(a), above, sorghum, (b), below, corn. (From Pallas and Bertrand, 1966).

Dixie 82, started closing its stomata at lower tension than the other corn lines. Although, complete closure was not observed until soil moisture tension reached the same value as the other lines. Both corn and sorghum started closing their stomata at about 0.3 atmospheres soil moisture tension. Corn was completely closed at 0.8 to 1.0 atmospheres. Sorghum was not completely closed until soil moisture tension reached 6.0 to 7.0 atmospheres.

We evaluated the relationship between stomatal resistance and leaf water potential in sorghum, pearl millet and corn by severing the vascular system near the ground and following the effect of drying by leaf measurements with a pressure porometer (Alvim, 1965, 1966) and thermocouple psychrometers (Box, 1965a,b).

The pressure porometer was used by imposing a pressure of 100 mm Hg on the leaf and the pressure reduction in 15 seconds recorded. A reduction from 100 to about 90 mm could be accounted for by leaks in the system, therefore a reading of 90 was taken to indicate fully closed stomata. Water potentials were measured on leaf discs taken immediately after the porometer readings. The relationship between porometer readings and water potential in a sorghum variety is shown in Figure 2. When the vascular system was cut there was a decrease in stomatal resistance and an increase in water potential. This is believed to be due to release of xylem sap tension as previously reported by others (Meidner, 1965).

Table 1 shows the results of water potentials of field grown sorghum, pearl millet and Conico* corn with stomata fully open and point of closure, as determined by the procedure defined above. Conico corn

* A drought resistant corn from Mexico, courtesy of Dr. John Lonquist, 7th generation, unselected, open pollinated at Lincoln, Nebraska.

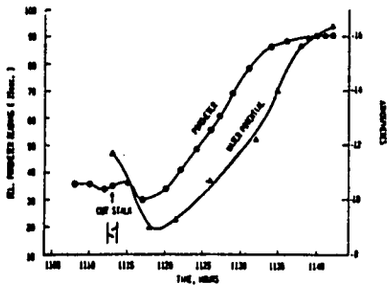

FIGURE 2

Effect of decreasing water potential on the relative leaf porosity (stomatal closure) of sorghum Combine Kafir-60 in the field, second leaf from top, air temperature 86.5 F, 64% relative humidity, a clear day, August 2.

TABLE 1

Leaf water potentials (atms.) of field grown sorghum, pearl millet and corn with stomata open and at point of closure as determined with a pressure porometer. Values are means of three determinations on each variety.

open	closed
4 Sorghums	
−14.4±.2 a*	−15.4±.1 a*
4 Pearl Millets	
−12.1±.7 b	−14.0±.2 b
Conico Corn	
−14.4±.5 a	−15.6±.3 a

stomatal response was very similar to sorghum in this case, which may be indicative of its greater drought resistance. Pearl millet was the most sensitive to reduced water potentials.

Sanchez-Diaz et al. (1969), in agreement with Pallas and Bertrand, found with porometer measurements that during a soil drying cycle the stomata of corn closed earlier than in sorghum. Other measurements by Sanchez-Diaz et al. (1970) indicated that stomatal closure took place at higher leaf water potentials for corn than sorghum, but when reduced transpiration in sorghum occurred it was more efficient in terms of rate and proportional decrease. Under normal watered conditions sorghum lost 2 to 3 times more water than corn from cut leaves, but cuticular transpiration was greater in corn than in sorghum. They concluded that differences in root exploration probably accounted for the different behavior of the two crops under drought conditions.

Soil Water and Roots

In Pallas and Bertrand's (1963) experiments Dixie 82 corn line was said to have a much smaller root system than the other lines observed. It was suggested that it could not absorb enough water to meet the evaporative demand and the stomata therefore closed earlier. This was thought to contribute to a prolonged period of soil moisture availability, and therefore, increased seasonal drought resistance. This is contrary to the general concept that a profuse root system is most desirable for drought resistance.

We compared soil water potentials in field plots of sorghums RS-610 and DeKalb C-42y, a drought resistant yellow hybrid, under unirrigated conditions in Nebraska in

* Values followed by the same letter in a column are not significant at the 5% level. Differences among the four sorghums (RS-610, CK-60A, CK-60B, C. 7078) and four millets (HB-1, Bil-3B, Tift 23A, Tift 23B) were not significant.

mid-August, 1969. Leaf water potentials and leaf diffusive resistances were also measured at the time the soil samples were taken. Water potentials were determined on leaf discs with thermocouple psychrometers and leaf resistances with a portable diffusion resistance meter (van Bavel et al., 1965; modified by Biggs et al., 1969). The sorghum was grown in 20 inch rows and hand thinned to 51,000 plants per acre. Table 2 shows the results of the experiment. The hybrid C-42y extracted soil moisture to a much lower water potential than RS-610 in the same period of time.

TABLE 2

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.

Hybrid	Soil Water Potential (atms.)*			Leaf Water Potential (atms.)**	Leaf Diffusive Res. (sec/cm)***
	depth, inches				
	12	24	36		
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 3 samples each from the middle of 4-row, 20 feet length plots and two replications.
** Mean values of 2 samples of 10 leaf discs (1-cm.) per sample (10 plants) and four replications. The second fully expanded leaf from the top sampled.
*** Means of 10 leaves (10 plants) in each of four replications. The second fully expanded leaf from the top measured.

The difference was particularly noticeable at 24 and 36 inches depth. This was reflected in slightly lower leaf water potentials and higher leaf diffusive resistances in C-42y.

Soil moisture extraction profiles may differ in varieties under irrigated or unirrigated conditions in both corn (Bruce et al., 1969) and sorghum. An example with sorghum is shown in Figure 3 in which

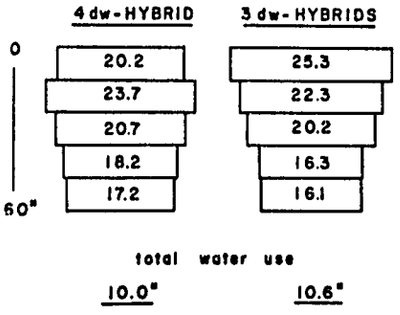

FIGURE 3

Soil water extraction profile for two 3-dwarf grain sorghum hybrids (averaged) compared to a 4-dwarf hybrid, at maturity, under dryland conditions in Israel. Numbers represent percent of total water use (to a depth of 60 inches) in each of the 12 inch soil depth increments. Each value represents six soil samples.

3- and 4-dwarf sorghum hybrids are compared. The 4-dwarf extracted proportionally less water at the 12 inch depth and proportionally more at 24 to 60 inches than the 3-dwarf hybrids.

A question to consider is whether a more or less profuse root system is desirable for drought conditions. Under moderate drought or short severe drought, the profuse root system may continue to provide for the shoot, but in a protracted, severe drought, it may exhaust the available moisture and succumb to the drought. The desirability of type of root size and development may depend on the climatic region and

expected frequency and duration of the drought. If the plant has greater heat and desiccation tolerance, a smaller root system may be more desirable during a long drought than a more profuse root system.

Desiccation and Heat Tolerance

Martin (1930) recognized that there may be differences in sorghum and corn to withstand and recover from greater tissue desiccation, but no direct measurements were made. Martin et al. (1931), however, examined the osmotic values of cell sap expressed from both sorghum and corn. They found a higher osmotic value in corn leaves than sorghum, but the stalks, crowns and roots of sorghum had higher osmotic values than corn. It was recognized that the higher osmotic value in the roots of sorghum may aid it in resisting desiccation. One would also expect the higher osmotic values of corn leaves to give it greater desiccation resistance, however, inability to adequately absorb and retard water loss apparently permits desiccation to occur below the injury level.

We have found osmotic potential differences within sorghum varieties which significantly affect their desiccation and heat tolerance (Table 3). It should be mentioned that the difference in heat and drought tolerance between Combine Kafir-60 and RS-610 was an exception in these experiments and was not found in many later experiments. Nevertheless, the differences was real in this case.

In our laboratory a simple screening technique has been developed for measuring heat and desiccation tolerance. The test is based on the fact that when plant cells are injured electrolytes diffuse out of the cells. The tissue is bathed in deionized water and after a specific time the electrical conductivity of the water is measured. The procedure of the test has been described (Sullivan and Kinbacher, 1967; Kinbacher et al. 1967; Sullivan et al., 1968). Results by this test have been shown to agree very well with

TABLE 3

A comparison of the water potential and osmotic potential with drought (percent injury after 24 hours equilibration with 94% relative humidity) and heat tolerance (temperature causing 50% injury) in sorghum. Water potentials and osmotic potentials were determined with thermocouple psychrometers before and after freezing respectively. Desiccation and heat injury was determined by the electrical conductivity method with leaf discs.

Sorghum	Water Potential (atms.)	Osmotic Potential (atms.)	Injury 94% R.H. (%)	Temp. at 50% Injury (°F)
CK-60	−12.0±.3	−20.0±1.6	26±2.2	120.6±.4
RS-610	−12.0±.4	−16.0±1.0	48±4.1	116.8±.4

Values are means of three replications, six plants sampled each rep.

TABLE 4

Heat and drought tolerance tests of field grown sorghum and Conico corn by the electrical conductivity method, and water potentials at 50% desiccation injury, estimated visually on whole leaves, July 25-27.

Sorghum	Percent Inj. (1) at 118.4 F	Percent Inj. (1) at 93% R.H.	Water Potential (2) at 50% Dirt. Inj. (atms.)
CK-60A	42.7 a*	68.7 a*	−44.0–44.4
M.35-1	45.3 a	60.1 b	−46.6–48.0
RS-610	50.3 a	78.1 c	−34.0–35.5
CK-60B	66.6 b	77.3 c	−35.0–36.0
C. 7078	78.3 c	70.5 ac	−36.4–38.5
Conico Corn	41.6 a	68.5 a	−46.0–47.2

(1) Means of 4 replications.
(2) Range of 2 replications.
* Means followed by the same letter in a column are not significant at the 5% level. Duncan's new multiple range.

total heat tolerance of intact plants (Sullivan et al., 1968).

Desiccation tolerance is known to often correlate with heat tolerance (Levitt, 1956). Results by the conductivity method showed that a number of species with known field drought resistance also had the highest heat tolerance. Sorghum had as much as 6 F higher heat tolerance than several vegetable crops (Sullivan et al., 1968).

Table 4 shows a comparison of heat and drought tests of sorghum and Conico corn by the electrical conductivity method. There is a clear relationship evident between heat and desiccation injury in this experiment. When the water potential of leaves was measured in plants wilted to the point where only 50 percent of the leaf tissue recovered turgidity when stood in water, the sorghums which had the higher heat tolerance recovered from greater leaf desiccation. Conico corn also agreed in this respect.

The chlorophyll stability index (C.S.I.) is another example of relating drought resistance to heat stability (Kaloyereas, 1958). Kilen and Andrew (1969) reported highly significant correlations between firing index of corn in the field and two types of heat tests. One of these was the chlorophyll stability index. The other was with seedlings (4-leaf stage) placed in a forced-air dryer at 54.5 C and 15-20% relative humidity for 5 hours. Recovery was estimated visually.

Julander (1945) heated range and pasture grasses in glass tubes in a water bath and from recovery counts he also concluded that heat resistance was a measure of drought resistance. Williams et al. (1969) also positively correlated results of heat chamber tests with field drought resistance of sweet corn.

We compared the chlorophyll stability index with the conductivity method with leaf discs and found good agreement between the methods when the procedure for chlorophyll stability index was carefully performed. Table 5 shows the results of one of these comparisons. The procedure for C.S.I. was es-

sentially the same as that of Koleyoreas (1958) as modified by Murty and Majumder (1962). The

TABLE 5

Chlorophyll stability index (C.S.I.) and heat tolerance (percent injury at 118.4 F) of leaf discs of sorghum, corn and pearl millet. Values are means of four replications.

	Sorghum		Corn	Millet
	M.35-1	RS-610	N-705	Tift 23B
C.S.I.	.061	.101	.047	.021
Heat tol.	31.1	50.3	27.0	12.8

two methods gave comparable results, but the conductivity method was much easier to perform and many more samples could be conveniently handled at one time. In these tests pearl millet had the highest heat tolerance, followed by corn and sorghum. The sorghum M.35-1*, a drought resistant sorghum from India, had significantly higher heat tolerance than RS-610. Corn was also significantly higher in heat tolerance than RS-610. This result seemed a little puzzling since sorghum is known for higher heat and drought resistance than corn. It may not be difficult to understand, however, if we recall the results and discussion on transpiration control. First, pearl millet and corn both closed their stomata sooner than sorghum when under water stress. Plants which tend to close their stomata under drought might be expected to have higher heat tolerance in response to increased leaf temperatures. Fast stomata closure on exposure to drought may, therefore, act as a selection pressure for heat tolerance under natural or artificial evolution.

Photosynthesis

When the temperature optimum for photosynthesis by intact plants or leaves of sorghum and corn has been compared, sorghum is reported to have a higher optimum than corn (Hesketh and Moss, 1963; Waggoner et al., 1963; El-Sharkawy and Hesketh, 1964; Idso and Baker, 1967). The increased photosynthesis rate with increased temperature may be partly due to decreased stomatal resistance; at temperatures over the optimum increased diffusive resistance to carbon dioxide may decrease the rate (Moss, 1963). That is, the initial effect of temperature on reducing net photosynthesis may be due to stomatal closure. As the temperature continues to increase then there may be direct effects on the photochemical apparatus. It has also been suggested that increased temperatures may increase respiration and internal carbon dioxide to concentrations which induce stomatal closure (Meidner and Mansfield, 1965).

We have tested the thermal stability of some photosynthetic reactions by isolated chloroplasts and found pearl millet the most stable, corn next and sorghum the least stable (Sullivan and Eastin, 1969). This result was in agreement with the conductivity test with leaf discs.

Blum and Sullivan (1971) measured the photosynthesis rates of sorghums RS-610 and M.35-1 leaf

* M.35-1 courtesy of Leland R. House, Rockefeller Foundation, New Delhi, India.

sections in a closed system in which atmospheric stress was controlled and carbon dioxide concentration held constant (Figure 4). Variety M.35-1 was reduced less at greater internal water stress than RS-610

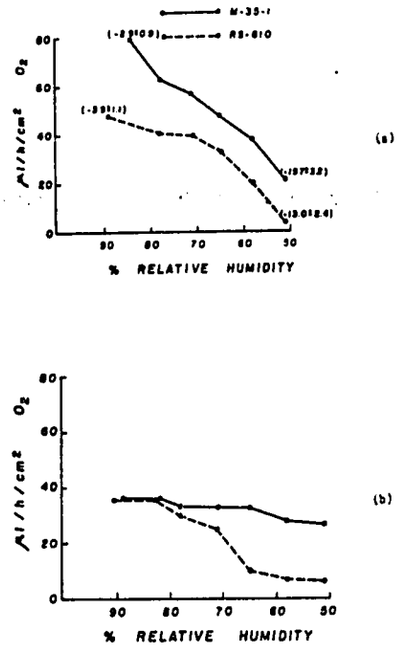

FIGURE 4

Net photosynthesis in two sorghum varieties as affected by percent relative humidity, at two light intensities (numbers in parentheses indicate leaf water potential in bars ± S.E., at highest and lowest % R.H.) (a), above, high light intensity, 0.14 uE cm^{-2} sec^{-1}. (b), below, low light intensity, 0.05 uE cm^{-2} sec^{-1}. (From Blum and Sullivan, 1971).

at high light intensities (about 7,000 foot-candles). The reduction was less noticeable at low light intensities. In that same study and with seven varieties of sorghum, decreased photosynthesis was observed at about -5 to -6 atmospheres leaf water potential. Boyer (1970) found photosynthesis in corn decreased at leaf water potentials below -3.5 bars.

Carlson (1969) working with low light intensity found carbon dioxide uptake continued in sorghum at a fairly steady rate until a severe stress of about -19 to -20 atmospheres leaf water potential occurred, then it dropped rapidly. Baker and Musgrave (1964) showed reductions of net photosynthesis in corn of up to 40 to 50 percent at slight soil moisture tension, one atmosphere or less. This result may reflect the faster stomatal response of corn to moisture deficits than in sorghum.

The contribution of photosynthate by the ear of corn and head of sorghum may also differ. Allison and Watson (1966) reported greater photosynthesis by the wheat ear than by the corn ear. Eastin and Sullivan (1969) reported significant contributions by photosynthesis of sorghum heads. Jennings and Shibles (1963) suggested contributions of oat heads to grain yield of 26 to 63 percent. It would be expected that the position of the sorghum head and flag leaf with respect to receiving light, as compared to the position of the corn ear, would enable them to contribute more photosynthate to grain yield. Under water stress lower leaves often attain early senescence making the expected contribution of the head and flag leaf even greater.

Stage of Development

Stage of plant development when the drought stress occurs must also be considered. Corn appears to be more susceptible to drought injury at pollination (Robins and Domingo, 1953; Denmead and Shaw, 1960). Soil moisture conditions during the period of flowering and early grain formation are particularly critical, however, for both corn and sorghum (Salter and Goode, 1967).

Whitman and Wilson (1965) found the floral apex of sorghum may develop at water stress sufficient to prevent leaf expansion, and also that infloresence development could be suspended during stress and resume development when rewatered. Volodarski and Zinevich (1960) also claimed a similar phenomenon occurred in corn in which retardation of ear initiation during stress was completely reversible. Robins and Domingo (1953) and Denmead and Shaw (1960) concluded that corn is relatively tolerant to stress in the vegetative stage. They suggested that the indeterminant nature of corn ear development may also lend itself to recovery from water stress.

Conclusions

1) Corn stomata are more sensitive than sorghum stomata to decreased soil water potentials. It seems that sorghum posses the ability to maintain a higher leaf water status and transpiration rate under increased drought stress, as compared to corn.

2) Corn leaves are more heat tolerant than sorghum leaves. This seems to be negatively associated with the above perhaps in an evolutionary sense.

3) There are some indications that sorghum is more drought resistant than corn due to differences in root traits. Higher osmotic potentials of the roots may be one.

4) Length and profuseness of roots does not automatically induce a superiority under drought. Type, intensity and duration of drought must be considered together with the drought resistance traits of the shoot.

5) Both corn and sorghum seem to be fairly sensitive to a drop in net photosynthesis with decreased leaf water potentials. The results described indicate that corn is more sensitive than sorghum in this respect, especially in regard to differences between the species in stomata response to stress. Variability was shown within sorghums in photosynthesis response to changes in leaf water status.

6) Before breeding for drought resistance is undertaken, the pattern, degree and timing of stresses under which the plant is to be grown in the field should be assessed.

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