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To the Graduate Council:

I am submitting herewith a dissertation written by William Keith Wesley entitled "Physiological Responses of Corn and Grain Sorghum Under Moisture Stress and During Rewatering." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Agricultural Plant and Soil Science.

John H Reynolds
Major Professor

We have read this dissertation and recommend its acceptance:

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Accepted for the Council:

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PHYSIOLOGICAL RESPONSES OF CORN AND GRAIN SORGHUM UNDER MOISTURE STRESS AND DURING REWATERING

A Dissertation

Presented to

the Graduate Council of

The University of Tennessee

In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

by

William Keith Wesley

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ABSTRACT

Grain sorghum (Sorghum bicolor (L.) Moench) and corn (Zea mays L.) seedlings were grown hydroponically for two weeks in a growth chamber. Moderate and severe moisture stress treatments were then applied to the plant roots by additions of polyethylene glycol to the growth media. After six days of moderate and three days of severe moisture stress, the osmotica were replaced with nutrient solution only. Changes in shoot length, weight, leaf water potential, and protein, nucleic acid and carbohydrate content were measured prior to, during and following exposure to moisture stress conditions. The effects of moisture stress and rewatering on these parameters were compared within and between species in an attempt to learn more about the species' drought resistance.

Grain sorghum seedlings exhibited larger reductions in leaf water potentials during stress periods than corn. Shoot elongation was retarded more in corn by smaller decreases in leaf water potential than in sorghum. Dry matter and protein accumulations of grain sorghum were not affected during the moderate stress period but were significantly reduced in corn. Dry matter and protein accumulations were reduced the same in both species during the severe stress period. Upon rewatering, the leaf water potentials of both species returned to normal. Dry matter and protein accumulations following exposure to moderate stress were the same in both species. Dry matter accumulations were the same in both species during and following exposure to severe stress, however, protein concentrations were lower in sorghum than in corn. Total RNA and DNA contents per unit dry weight were not affected by either moisture stress

or rewatering. Water stress had no consistent effect on either total sugar or total nonstructural carbohydrate content of either species.

The internal water status of grain sorghum appeared to be characteristic of a drought resistant plant species. Growth responses following exposure to water stress were the same in both corn and grain sorghum. Total RNA and DNA concentrations were not affected by moisture stress conditions in either species, but protein concentration was affected more in sorghum than corn during recovery from severe stress. No major biochemical differences were found between corn and grain sorghum that would explain sorghum's greater ability than corn's to resist drought under natural conditions.

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CHAPTER I

INTRODUCTION

Grain sorghum (*Sorghum bicolor* (L.) Moench) has long been considered to be one of the most drought resistant crop plants (19, 33), although the reasons for its drought resistance are not well established. Corn's (*Zea mays* L.) grain production potential is slightly greater than grain sorghum's potential when grown under optimum environmental conditions (13). In Tennessee, dry matter production of shoots in corn and grain sorghum are about equal under optimum environmental conditions (5). The center of grain sorghum production in the United States is the semi-arid Great Plains region. The development of grain sorghum production in this region indicates that the crop will withstand drought conditions better than corn (20).

Only a few studies have been conducted to explain sorghum's superiority in drought resistance to corn. Morphological comparisons of these two species have been made (29, 32). Sorghum was found to have twice as many secondary roots in proportion to leaf area as corn. It was generally believed that sorghum's more efficient control of water absorption and transpiration were major factors contributing to its superior drought resistance. More recently, extensive investigations (36, 37, 38, 39, 40) of the effects of water stress on transpirational and stomatal behavior of corn and grain sorghum, in which differences in rooting habits were suppressed, have indicated that sorghum exhibits a smaller reduction in water content for a given reduction in leaf water potential than corn.

These results only partially characterize the superior drought resistance of sorghum over corn. A rather large number of reports have appeared in recent literature pertaining to the effects of water stress on physiological and biochemical processes of corn and other crop species. However, no investigations have been reported in which the effects of water stress on biochemical constituents of corn and grain sorghum were studied and compared. Possibly there are some biochemical differences between these two species that may give some indication of sorghum's ability to resist drought better than corn. The objective of this study was to investigate growth, physiological and biochemical responses of corn and grain sorghum seedlings to water stress and recovery upon rewatering. Changes in shoot elongation, weight, leaf water potential, and protein, nucleic acid and carbohydrate content were measured. The effects of water stress and rewatering on these parameters were studied and compared within and between each species in an attempt to learn more about the differences in drought resistance.

CHAPTER II

LITERATURE REVIEW

The literature dealing with the effects of water stress on plant growth and physiological processes is extensive, and numerous reviews have been devoted to this subject (8, 9, 14, 22, 23, 31, 44, 45, 48). Recently, Levitt (25) reported and evaluated all of the theories on drought resistance in plants. There are only a few papers in the literature that directly compare the effects of water stress on corn and grain sorghum.

Almost every plant process is directly or indirectly affected by the water supply, since all plant processes take place in what is effectively an aqueous medium. Water is involved as a transporting agent and is a reactant in many of these plant processes. An inadequate water supply is often a limiting factor to plant growth. Water deficits affect practically every aspect of plant growth by modifying the plant's anatomy, morphology, physiology and biochemistry. Plant growth is influenced directly by plant water stress and indirectly by atmospheric and soil water stress. The only reliable indicator of the severity of drought in respect to plant growth is the degree of water stress developed in the plants under consideration (22).

Plant water stress or water deficits refer to situations where cells are less than fully turgid. The most general effect of prolonged water stress on plants is a general reduction in turgidity and hence cell enlargement (21).

Miller (32) compared the drought resistance of corn and grain sorghum from a morphological point of view. He found sorghum plants had twice as many secondary roots per unit of primary roots as did corn. Sorghum's primary and secondary roots were more fibrous than corn's. Sorghum had only half the leaf area exposed to evaporational and transpirational water loss as corn. Therefore, the more fibrous root system and smaller leaf area of sorghum were considered to be factors favoring the maintenance of a balance between water absorption and transpiration.

Martin (29) reported that the basal buds of sorghum plants have the ability to remain dormant during periods of drought and tiller rapidly when the water stress is released, whereas corn plants do not possess this ability. He observed that sorghum stalks retained more water during water stress periods than corn, and thus extended the life of the tiller buds. Martin also noted that sorghum leaves and stalks are covered with more wax, and are more completely cutinized than corn. Grain sorghum leaves have groups of hygroscopic cells in single rows along each side of the midrib which cause the leaf to fold, rather than roll as do corn leaves, when plant water deficits develop. The folding of sorghum leaves takes place much faster than the rolling of corn leaves, thus reducing transpirational water losses faster when water stress develops (29). The upper leaf surfaces of both corn and sorghum have two-thirds as many stomates as the lower leaf surfaces (29). Sorghum leaves have been reported to have from 50% (29) to 200% (36) more stomates per unit surface area than corn leaves, although the stomates of sorghum leaves are only one-half to two-thirds (36) the size of corn stomates.

In a recent study comparing the behavior of corn and grain sorghum during and after moisture stress, Sanchez-Diaz and Kramer (36) took into account that sorghum plants have a more efficient root system by allowing the roots of each species to completely occupy the growth containers prior to the induction of the water stress. They found the water status, measured as leaf water potential by a thermocouple psychrometer, and water saturation deficit of sorghum was superior to that of corn. Sorghum exhibited a smaller reduction in water content (lower water saturation deficit) for a given reduction in leaf water potential than corn. This response was considered characteristic of a drought-resistant plant species.

The transpiration rate of sorghum is generally higher than corn under adequate water supply conditions (29, 36, 43), however, under water stress conditions the transpiration rate of sorghum is reduced faster than in corn (36, 38, 39, 43). Sanchez-Diaz and Kramer (36) found the stomates of corn close at a higher water potential than the stomates of sorghum, but more water was transpired in corn because of a slower closing rate as stress became more severe.

Glover (11) compared the stomatal behavior of corn and sorghum under moisture stress conditions in Kenya, East Africa. Stomatal aperture and apparent carbon assimilation measurements were made at two stages of growth, when the plants were young and approaching tasseling. The plants were exposed to both short (3 to 4 days) and long (7 to 10 days) periods of the severe natural drought conditions of the area. Corn stomates were markedly affected by exposure to long periods of severe moisture stress conditions. Although the leaves regained turgidity rapidly upon rewatering, their apparent pattern of normal stomatal behavior was not restored. Sorghum stomates recovered after 14 days of severe moisture stress conditions. Severe drought was found to be less deleterious to young corn plants than to old plants, whereas the stage of maturity of sorghum plants was immaterial. Glover suggested that the rapid recovery of sorghum stomates after exposure to severe drought partly accounts for the superiority of its drought resistance in dry regions. Slatyer (43) reported that sorghum has a better-developed root system, more effective control of transpiration and a slower decrease in turgor than cotton and peanuts growing under the same environmental conditions.

During the past few decades there have been substantially more reports appearing in the literature pertaining to the physiological and biochemical effects of moisture stress on corn than on sorghum. West (49) explored the effect of various degrees of water stress, simulated by mannitol solutions, on growth, protein, nucleotide and RNA metabolism of corn seedlings propagated in the dark. Growth as measured by fresh and dry weight changes was reduced quantitatively by water stress with a concurrent reduction in protein and nucleotide content per seedling. Total RNA content was found to increase in the stressed seedlings.

Shiralipour and West (42) studied the effects of water stress on the amino acid, protein and DNA content of corn. They found that moderate water stress lowered the protein content of the corn seedlings as compared to well-watered seedlings. However, the protein content continued to increase with time but at a reduced rate. Under severe moisture stress conditions protein synthesis decreased and protein degradation increased. The DNA content of the seedlings was not influenced by either the moderate or severe moisture stress regime, thus the genetic mechanisms of the corn plants were not influenced by water stress.

West (50) later studied the effects of mannitol-simulated moisture stress on the growth, protein and RNA contents of corn seedlings. He found that the RNA content of the seedlings increased under stress conditions and that a large part of this increase occurred in the ribosomes. Drought stress did not affect the base composition of the ribosomes but did reduce polysome formation. Reductions in polysome formation were probably a result of inadequate messenger RNA synthesis.

Hsiao (15) reported that polysomes in corn seedlings shifted rapidly from the polymeric to the monomeric form during moisture stress. This shift could affect protein synthesis and ultimately plant growth. However, preliminary data obtained from the development of a method for rapidly monitoring extensive growth of intact leaves during water stress by Hsiao, Acevedo and Henderson (16), suggest that changes in polyribosomes by water stress seem to follow the change in growth, not precede it.

Acevedo, Hsiao and Henderson (1) reported that reduced growth of corn leaves from exposure to short and mild water stress was a result of turgor loss in the leaves that was necessary for expansive growth. Reduced growth during water stress was not a result of metabolic alterations. Growth was stopped due to loss of turgor before CO_2 assimilation was reduced and before any noticeable increases in ribonuclease and amylase activities occurred. They suggested that many of the observed metabolic alterations caused by water stress arise indirectly as a result of reduced growth, especially during the initial stages of water stress.

Maranville and Paulsen (28) studied the alterations in carbohydrate composition of corn seedlings under moisture stress conditions. Moisture stress had no effect on the fructose and glucose content, increased the sucrose content slightly, but markedly decreased the starch content of the seedlings. Although sucrose and starch synthesis were not affected by moisture stress, the enzymatic hydrolysis of sucrose was decreased while starch hydrolysis was increased. These latter responses were apparently survival adaptations to the water stress conditions and possibly helped the plants to retain turgidity and protect protoplasmic constituents.

Boyer (6) compared the sensitivity of photosynthesis in corn and soybeans at low leaf water potentials. He found that rates of photosynthesis in corn were inhibited whenever the leaf water potential dropped below -3.5 bars. He attributed the inhibition of photosynthesis in corn to stomatal behavior down to a leaf water potential of -10 bars, below which photosynthetic behavior was due to other additional factors.

Younis et al. (53) evaluated the effects of temperature and its interaction with moisture stress on the nitrogen metabolism of corn seedlings. They found that the interaction of temperature with moisture stress did not significantly affect the relative contents of nitrate, soluble protein-nitrogen, soluble nonprotein-nitrogen, and total organic nitrogen, but did affect the relative nonsoluble nitrogen content and nitrate reductase activity. Mattas and Pauli (30) found nitrate reductase activity of corn seedlings decreased sharply with a short exposure to high temperature and moisture stress. Total Kjeldahl nitrogen per plant increased rapidly during the initial stress period and remained fairly constant thereafter. Moisture stress also increased the incorporation of reduced nitrogen into nonsoluble forms much faster than into soluble protein forms.

CHAPTER III

EXPERIMENTAL PROCEDURES

Seed Germination

Corn (*Zea mays* L., 'Tenn. 5009') and grain sorghum (*Sorghum bicolor* (L.) Moench, 'DeKalb E-57') seed were germinated in covered plastic pans lined with six layers of paper towels saturated with 250 ml of 10^{-4} M $CaCl_2$. Corn seed were placed on the paper towels embryo-down, approximately 1 cm apart, and the grain sorghum seed were distributed at random approximately 0.5 cm apart. The seed in each pan were covered with one layer of moist paper towel for two days to insure the necessary humidity for uniform germination. The seed were germinated for three to four days and watered as needed with deionized water after which the seedlings were transferred to a growth chamber.

The growth chamber had a 3.25 sq. meter plant bed and was maintained at 30 C during a 13-hr light photoregime at approximately 60% relative himidity and 18 C during an 11-hr dark photoregime at approximately 90% relative humidity. The maximum light intensity from both fluorescent and incandescent sources was 33,000 lux.

Growth Tanks

The seedlings were propagated hydroponically in nine-liter capacity plastic growth tanks. Each tank was covered with one layer of 4-mil black plastic to retard light penetration and subsequent algae growth. The seedlings were inserted through small slits in 1.3 cm thick polyurethane foam discs with a diameter of 7.6 cm. Each disc supported five plants. The polyurethane foam discs were supported by a styrofoam lid, 32.4 cm in diameter and 2.54 cm thick, that fit inside the growth tank. Each growth tank contained nine polyurethane foam discs. The growth tanks were filled with half-strength Hoagland's #2 nutrient solution with the exception of full-strength $MgSO_4$ and FeEDTA. The nutrient solutions were changed every four days, except during the water stress treatment periods, and pans cleaned thoroughly with mild detergent and chlorox. Each growth tank was aerated by two gas-dispersion stones and the air flow to individual tanks was uniformly regulated by adjustable clamps.

Moisture Stress Treatments

Moisture stress treatments were induced 14 days after the seedlings were transferred to the growth tanks. The moisture stress treatments were: (1) seedlings subjected to less than one bar osmotic pressure (nonstressed control), (2) seedlings subjected to -5 bars osmotic pressure for six days (moderate stress), and (3) seedlings subjected to -10 bars osmotic pressure for three days (severe stress). The nonstressed control seedlings were grown in half-strength Hoagland's #2 nutrient solution only. Moderate and severe treatments were induced by increasing the osmotic pressure of the hydroponic growth medium by placing either a 15 percent or a 25 percent solution, respectively, of polyethylene glycol 4000 (Carbowax 4000, approximate molecular weight of 4000), dissolved in half-strength Hoagland's nutrient solution, in the tanks. The quantity of Carbowax 4000 that moved into the seedlings was not measured, and its effect on plant growth was assumed to be only a result of decreased water supply. Lawlor (24) carefully examined the problem of polyethylene glycol absorption and concluded that polyethylene glycols of 1000 or higher molecular weight were not absorbed in significant quantities by corn roots unless the root system was damaged.

The volume of the osmoticum was maintained as close as possible to nine liters during the treatment periods to prevent concentration changes and subsequent osmotic pressure changes. Moderate and severe water stress treatments were removed six and three days after induction, respectively, by replacing the osmoticum with nutrient solution only.

Control, moderate and severe moisture stress treatments were arranged in a randomized complete block design. Only three replications of each treatment were applied due to space limitations of the growth chamber. Therefore, the experiment was repeated for each species. Corn and grain sorghum were grown at different times due to large differences in their growth rates.

<u>Water Potential Measurement</u>

The water status of the plants was monitored by measuring the water potential of the plant tissue. A 0.6 cm leaf disc from the third or fourth leaf was placed in a Wescor Model C-51 thermocouple psychrometer chamber and microvoltage output recorded with a Wescor Model HR-33 Dew Point Microvoltmeter. The Microvoltmeter was calibrated at 30 C by placing 0.6 cm filter paper discs saturated with a series of NaCl solutions (30 C) of varying molarity and known osmotic potentials in the thermocouple psychrometer chamber. A standard curve was determined by plotting microvoltage output versus water potential. Leaf water potential measurements were made on two representative plants from each tank and reported in bars.

Measurement of water potential in plant tissue has gained wide acceptance in the past few years as a fundamental measure of plant water status. Leaf water potential is the chemical potential of water in the leaf, expressed as energy per unit volume, below the chemical potential of pure water at the same atmospheric pressure and temperature (23).

Sampling Methods and Periods

Plant samples were taken prior to, during and following the induction of the moisture stress treatments. Samples were collected two weeks after the seedlings were placed in the growth tanks after which the osmotically-induced moisture stress treatments were applied. The plants were subjected to three days of severe stress and six days of moderate moisture stress. Samples were taken two, three, six, ten, and fourteen days after the induction of the moisture stress treatments.

Samples were taken by harvesting the plant shoots above the first node. Dry matter percentage was determined for each sampling period by placing two plant shoots in a glass bottle sealed with a rubber stopper. The fresh weight of the sample was recorded after which the stopper was removed and the sample dried in a forced ventilation oven for 24 hr at 70 C. Four to six shoots were harvested and placed in a nonvented plastic bag and the fresh weight determined within 10 to 15 minutes and stored at -20 C for chemical analyses except for carbohydrate analyses which were made on the oven-dried samples. Root samples were not taken due to the extreme difficulty in separating the roots of different plants and, also, to prevent excessive damage to roots remaining after each sampling date that could possibly result in the absorption of polyethylene glycol.

Chemical Analyses

The frozen samples were initially prepared for analysis of TCA-insoluble protein, ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) by a modification of the procedure reported by West (49). The frozen tissue was cut into 1-cm segments and homogenized in 50 ml of cold deionized water in an Omnimixer at maximum speed for 5 minutes. Cell walls, nuclei and debris were removed by centrifuging at 3800 X g for 10 minutes. Protein was precipitated from aliquots of the cleared homogenate by the procedure reported by West (49) and analyzed for TCA-insoluble protein by the method of Lowry et al. (26) with bovine serum albumin protein standards. Total RNA was isolated from an aliquot of the cleared homogenate by the procedure reported by West (49) and determined by the difference in absorbance at 260 and 290 nm of the $HClO_4$ hydrolyzate according to the method of Ogur and Rosen (34) with modification for corn material (7, 12, 27). Deoxyribonucleic acid (DNA) was isolated from the RNA-free supernatant by the addition of an equal volume of 95% ethanol and analyzed by the cysteine hydrochloride procedure of Stumpf (46).

Total nonstructural carbohydrate and total sugar contents were determined on the dry matter samples. Replications of each treatment were combined on most of the sampling dates in order to obtain a sample large enough for carbohydrate analysis. Total sugars were extracted from dried shoot tissue with warm (50 C) 80% ethanol following the procedure used by Maranville and Paulsen (28). Total sugars were determined as glucose by the alkaline ferricyanide method of Ting (47). Nonstructural carbohydrates remaining in the residue after total sugars were extracted were hydrolyzed with 0.7 N HCl for three hr in a 100 C water bath and measured as glucose (47). Total nonstructural carbohydrates were calculated by adding the total sugar content to the nonstructural carbohydrate content remaining in the residue. No statistical analyses were applied to the results due to the lack of replication of treatments.

Statistical Analyses

Analyses of variance were applied to data from individual sampling dates for each species. Moisture stress treatment means were subjected to the Duncan's Multiple Range Test. Differences between the two species during treatment periods were compared by the use of a Paired t-Test. For tests of significance, a probability level of 0.05 was chosen unless otherwise stated in the results of this study. Correlation coefficients between selected variables were calculated.

CHAPTER IV

RESULTS

The degree of water stress that was developed in the plants by the osmotically-induced water stress treatments was measured as leaf water potential. Results are presented on the basis of treatment effects in most cases and will be related to leaf water potential.

Leaf Water Potential

The leaf water potential of grain sorghum plants prior to and during the moderate and severe stress periods and upon rewatering is shown in Table 1 and Figure 1A along with the nonstressed controls throughout the experimental period. The average leaf water potential of the nonstressed control plants throughout the experiment was -9.8 bars. Leaves of the control plants exhibited no visual signs of wilting during the two-week period. Exposure of the roots to six days of moderate (-5 bar) water stress resulted in a gradual decrease in the leaf water potential. The leaf water potential was approximately two bars less than the control after 24 hr of moderate stress and approximately six bars less than the control after six days. The rate at which the leaf water potential decreased during the moderate stress period was approximately one bar per day. Visual signs of wilting were evident 24 hr after exposure to moderate stress and some leaf tip necrosis was visible at the end of the six day stress period. The severe water stress treatment (-10 bar) caused a rapid decrease in the leaf water potential of the sorghum plants. Twenty-four hours of severe stress reduced the leaf water potential to -16.3 bars, or

Table 1. Leaf water potentials of grain sorghum seedlings prior to, during and following exposure to stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(bars)	
14[1]	-9.8a[4]	-10.0a	-9.8a
15	-9.7a	-11.9a	-16.3b
16	-10.5a	-12.8b	-17.8c
17[2]	-10.7a	-12.9b	-22.8c
18	-10.2a	-13.3b	-13.0b
19	-11.0a	-14.0b	-10.8a
20[3]	-8.8a	-14.4b	-9.7a
22	-9.7a	-10.5a	-10.0a
24	-9.8a	-10.2a	-10.1a
27	-9.3a	-9.3a	-9.4a

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

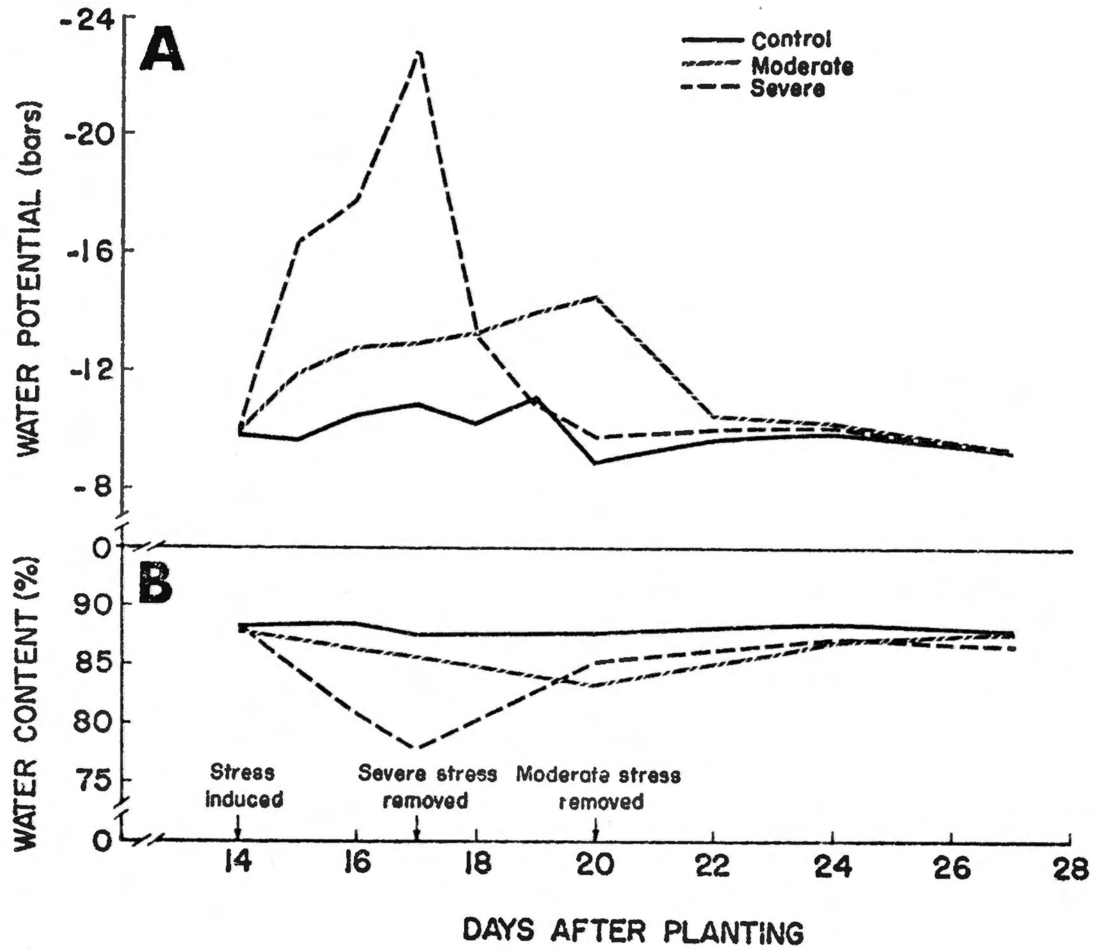

Figure 1. Changes in the water status of grain sorghum seedlings prior to, during, and following exposure to moisture stress conditions. Leaf water potentials and percent water content are shown in A and B, respectively.

6.5 bars below the control. By the end of the severe stress period, the leaf water potential was approximately 12 bars below that of the nonstressed control plants. One hour after the induction of the severe stress treatment the leaves began to wilt, and at the end of the three-day stress period all leaf tips were severely damaged. Upon rewatering the leaf water potentials of both moderately and severely stressed plants returned to values similar to the nonstressed control. Within 12 hr after rewatering leaves of plants from each treatment regained turgidity.

The leaf water potentials of corn seedlings subjected to the three moisture regimes are shown in Table 2 and Figure 2A. The average leaf water potential of the control plants was -10.9 bars, which was one bar less than the nonstressed grain sorghum plants (Table 1). Six days of moderate water stress resulted in a slow decrease in leaf water potential. The average leaf water potential was approximately 2.5 bars less than that of the nonstressed control at the end of the stress period. Reductions in leaf water potential by moderate stress were approximately 2.5 times greater in grain sorghum (Table 1) than in corn. As in grain sorghum, the severe water stress treatment caused a rapid reduction in the leaf water potential of corn, although the reduction was not as severe in corn as in grain sorghum. Twenty-four hours of severe water stress reduced corn's leaf water potential approximately five bars below the control, and three days of stress resulted in a seven-bar reduction. As in sorghum, the leaf water potentials of corn rapidly returned to values similar to the nonstressed control plants upon rewatering. Both water stress treatments caused leaf damage that remained evident throughout the recovery period, with considerably more damage to the severely stressed plants.

Table 2. Leaf water potentials of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(bars)	
14[1]	-10.9a[4]	-11.0a	-10.8a
15	-11.5a	-11.7a	-15.0b
16	-10.8a	-11.7b	-16.6b
17[2]	-10.6a	-12.2b	-16.9c
18	-10.7a	-12.4b	-12.6b
19	-10.8a	-12.4b	-10.3a
20[3]	-10.7a	-13.2b	-10.0a
22	-10.6a	-11.7a	-10.8a
24	-10.6a	-10.8a	-10.7a
27	-10.9a	-10.5a	-10.7a

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

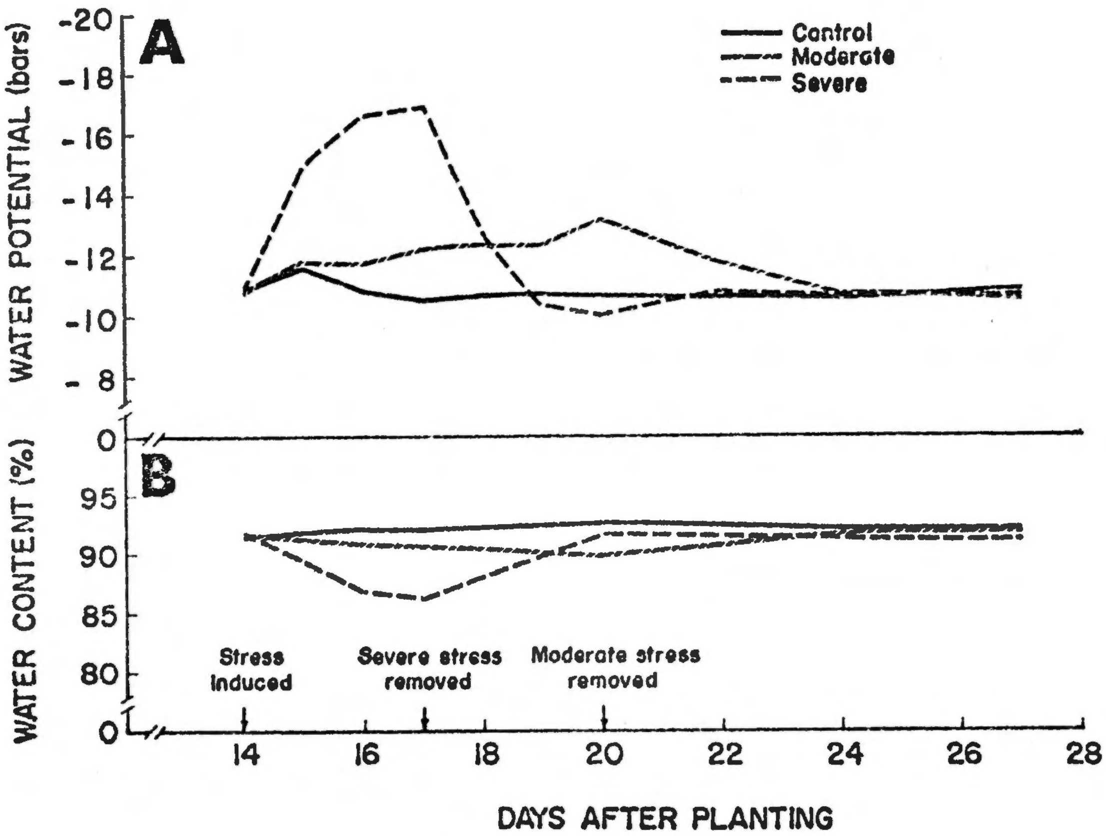

Figure 2. Changes in the water status of corn seedlings prior to, during, and following exposure to moisture stress conditions. Leaf water potentials and percent water content are shown in A and B, respectively.

Figures 1B (page 17) and 2B show the water contents of grain sorghum and corn seedlings, respectively, throughout the experimental period. As would be expected, the water content of the seedlings was less at the lower leaf water potentials. Water content was found to be highly correlated with leaf water potential in both corn (r = 0.94) and grain sorghum (r = 0.92).

Shoot Growth

Fresh weights per plant of grain sorghum seedlings prior to, during and following exposure to six days of moderate and three days of severe moisture stress conditions along with the nonstressed control plants are shown in Figure 3. Moderate water stress caused significant reductions in fresh weights of sorghum seedlings throughout the stress period as compared to the nonstressed control plants. Reductions in fresh weight by the moderate stress treatment ranged from 21 percent after two days to 32 percent after six days. Although the fresh weights were significantly lower during the stress period than the control seedlings, the seedlings were growing as indicated by the increase in fresh weight per plant at the end of the stress period as compared to the weight at the time the stress was induced. Upon rewatering, fresh weight per plant increased at a slightly faster rate than during the stress period. After one week of recovery, fresh weight of the seedlings subjected to moderate stress was 26 percent less than the nonstressed control seedlings. The fresh weights of the seedlings subjected to the severe stress treatment were 50 percent less than the control after two days. After three days of severe stress the fresh weights of the seedlings were 69 percent less than the non-stressed control seedlings. Unlike the moderately stressed plants, the

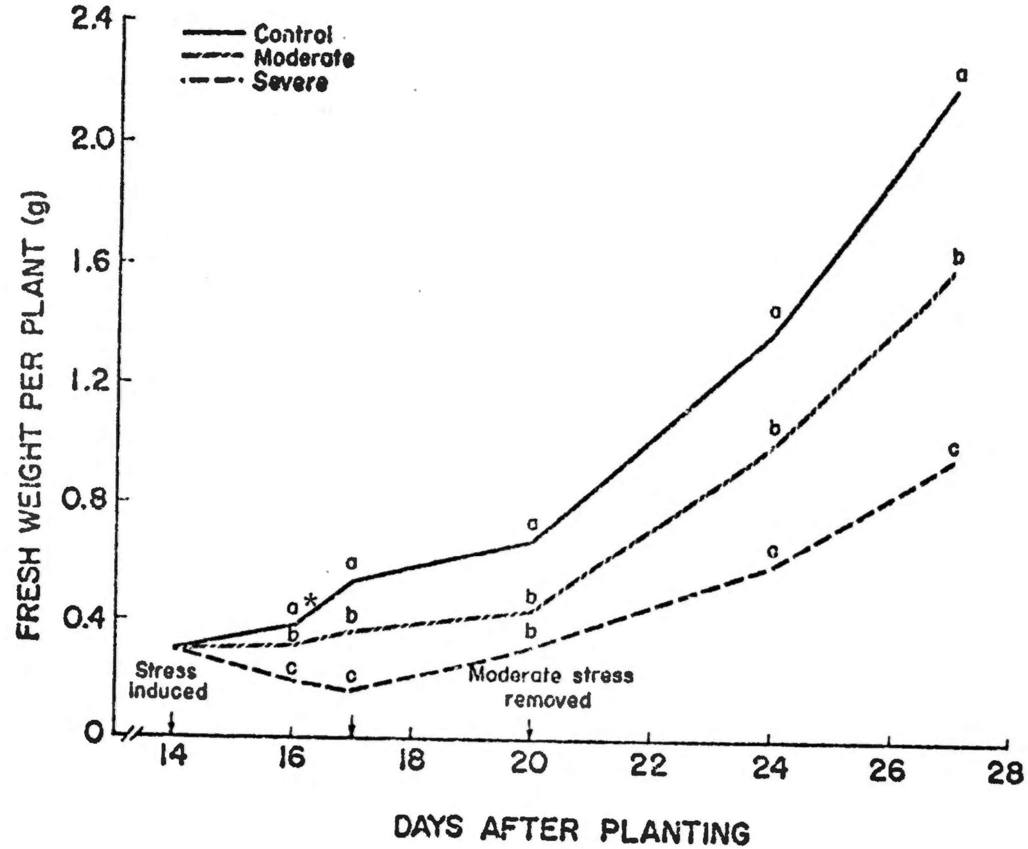

Figure 3. Fresh weights per plant of grain sorghum seedlings prior to, during, and following exposure to moisture stress conditions.

*Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

fresh weight of the severely stressed plants did not increase during the three day stress period. Upon rewatering the fresh weight of the plants subjected to severe stress began to increase and was 43 percent less than the control plants after 10 days of recovery. At the end of the recovery period, 27 days after planting, reductions in fresh weight of the grain sorghum seedlings subjected to three days of severe stress were twice as severe as reductions in fresh weight of plants subjected to six days of moderate stress.

Fresh weights per plant of corn seedlings prior to, during and following exposure to moisture stress conditions are shown in Figure 4. Three days of moderate water stress caused a significant reduction in fresh weight when compared with the nonstressed control plants. Reductions in fresh weight ranged from 18 percent after two days of moderate stress to 44 percent after six days. As did the grain sorghum plants (Figure 3), corn plants continued to grow during the moderate stress period but at a much slower rate than the nonstressed control plants. Upon rewatering the fresh weight of the moderately stressed plants began to increase at a much faster rate than during the stress period. Three days of severe stress retarded growth of the corn plants drastically. Reductions in fresh weight were 45 percent after two days and 60 percent after three days of severe stress. Fresh weight per plant of corn began to increase upon removal of the severe stress treatment. At the end of the 10-day recovery period the seedlings weighed approximately 43 percent less than the control plants. At the end of the recovery period, reductions in fresh weight of the corn seedlings subjected to three days of severe stress were approximately twice as much as the reductions in fresh weight of the seedlings subjected to six days of moderate stress.

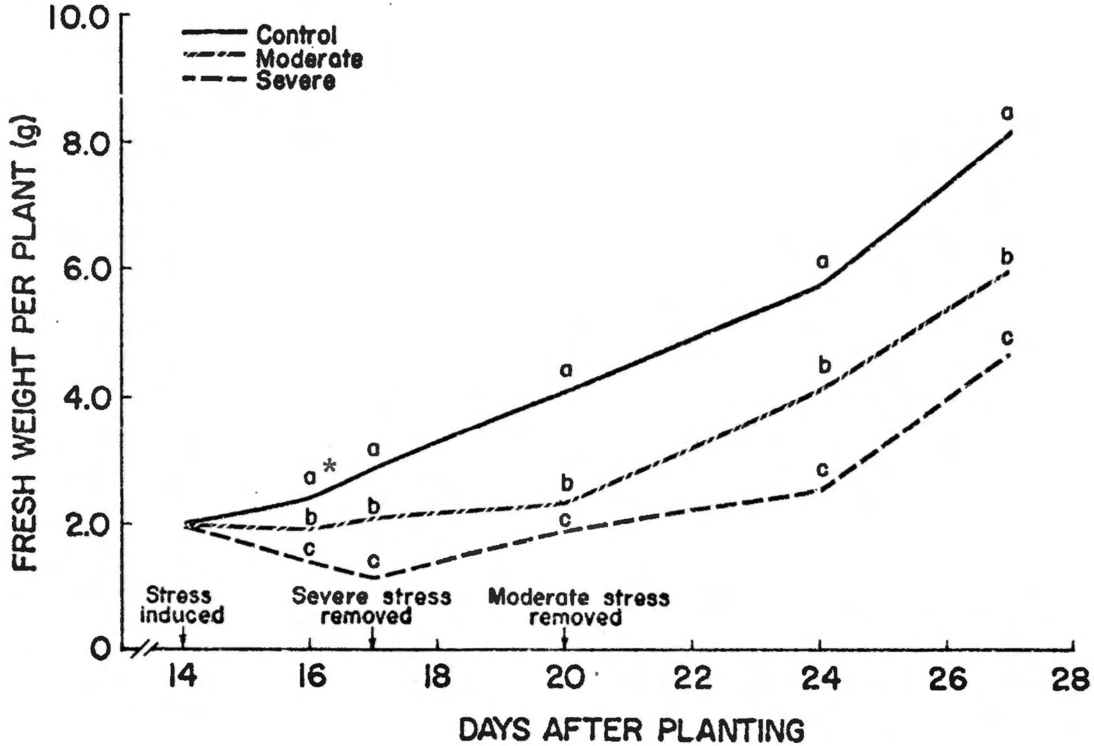

Figure 4. Fresh weights per plant of corn seedlings prior to, during, and following exposure to moisture stress conditions.

*Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

Figure 5 shows the dry weights per plant of grain sorghum seedlings prior to, during and following exposure to the three moisture regimes. The dry weight increases of the nonstressed control seedlings throughout the experiment were similar to those reported by Bartel and Martin (3). Six days of moderate stress had no significant effect on dry weight per plant during the stress period, but on each date the dry weights were lower than the nonstressed control plants. Three days of severe stress caused a 37 percent reduction in dry weight. Dry weights per plant after three days of severe stress were slightly less than at the beginning of the stress treatment. Therefore, the severely stressed plants were not growing during the stress period as indicated by the loss in dry weight, possibly because the plants were respiring metabolites already synthesized. As in the moderately stressed plants, dry weight increases upon rewatering were evident. By the end of the recovery periods of both stress treatments, reductions in dry weight were proportionally the same for each treatment as reductions in fresh weight. A comparison of the fresh and dry weights of sorghum plants in Figures 3 (page 22) and 5, respectively, shows that dry weight of sorghum plants was affected less than fresh weight during the stress periods, possibly because of the large reductions in water content (Figure 1B, page 17).

The dry weights per plant of nonstressed and stressed corn plants are shown in Figure 6. Three days of moderate stress caused no significant reductions in dry weight as compared to the nonstressed control plants, but the dry weights of the stressed plants were slightly less than the control. After six days of moderate stress, the dry weights of the corn plants were significantly reduced by 30 percent. Three days of severe

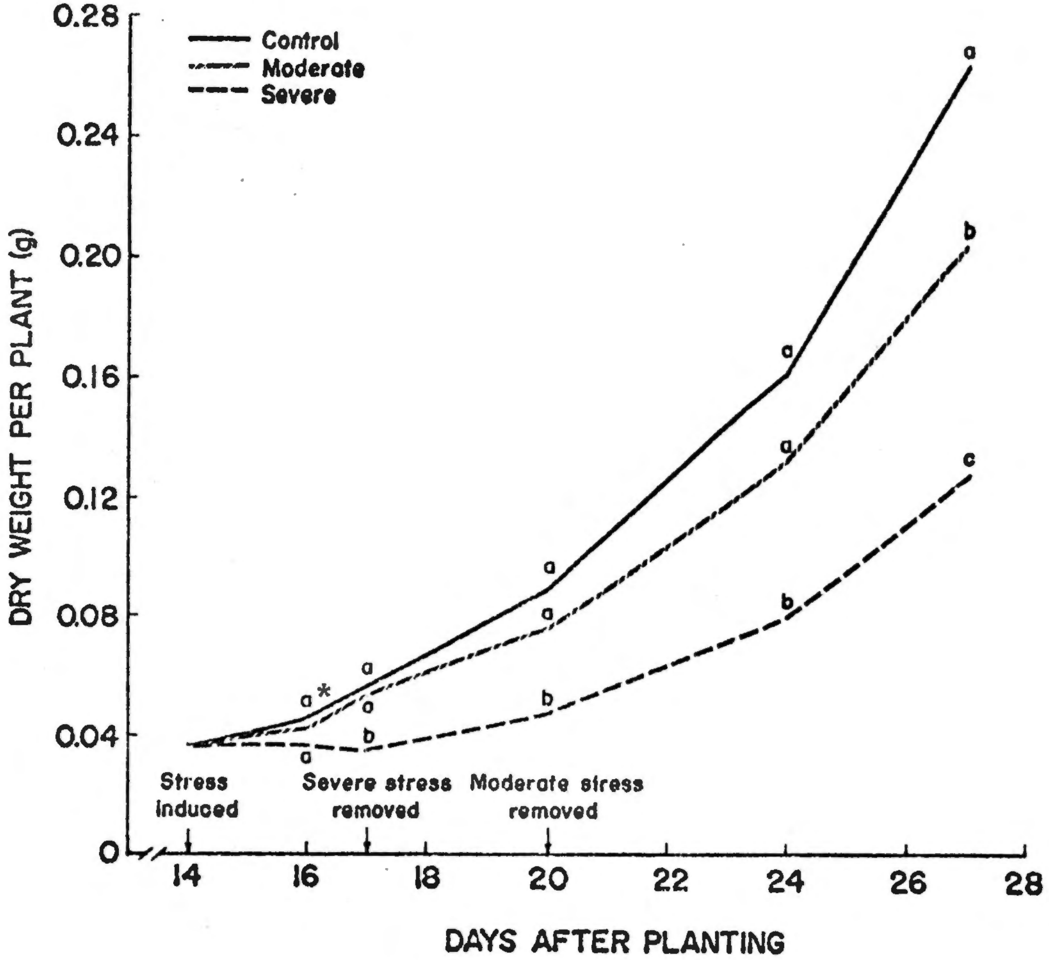

Figure 5. Dry weights per plant of grain sorghum seedlings prior to, during, and following exposure to moisture stress conditions.

*Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

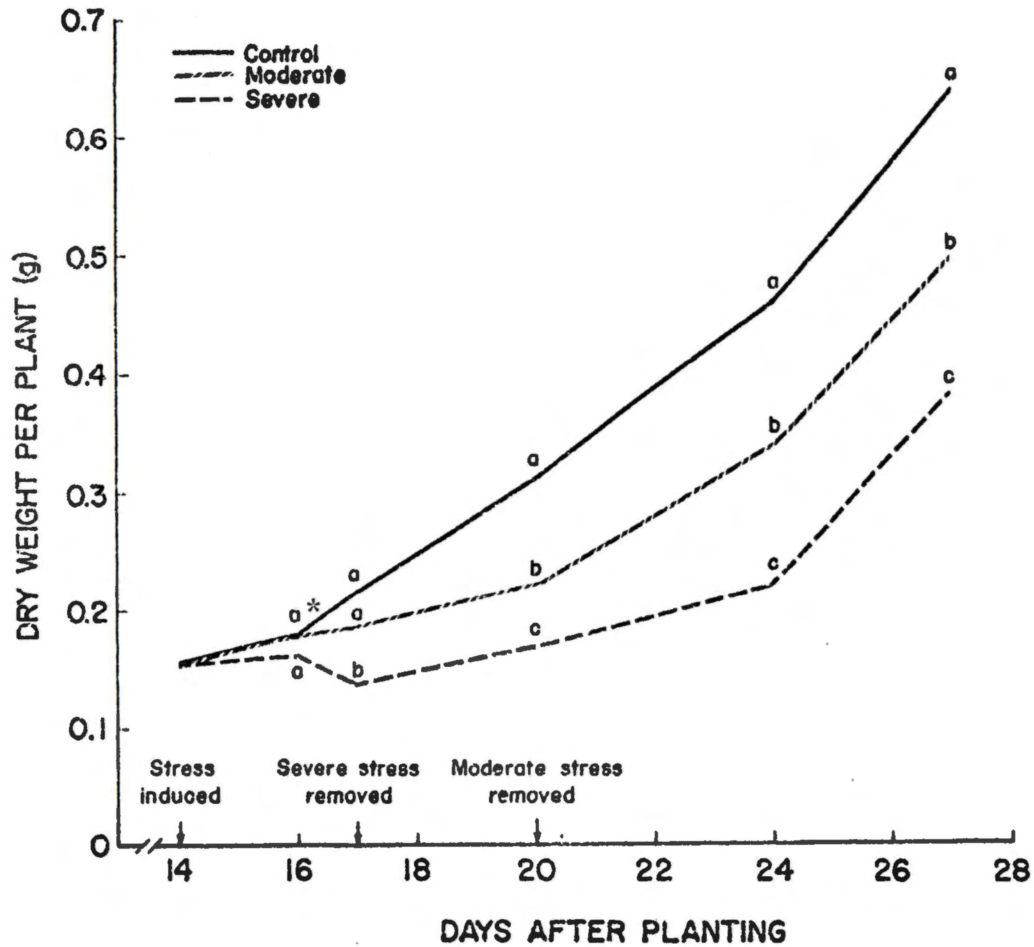

Figure 6. Dry weights per plant of corn seedlings prior to, during, and following exposure to moisture stress conditions.

*Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

stress reduced dry weight by 36 percent as compared to the control plants. The corn plants did not grow during the severe stress period as indicated by the decline in dry weight when compared to the dry weight of the plants at the time the stress was induced. Upon rewatering the dry weights of the moderately stressed corn plants increased at a faster rate than the severely stressed plants. At the end of the recovery period, the reduction in dry weight of the plants subjected to three days of severe stress was approximately twice as much as the reduction in dry weight of the plants subjected to six days of moderate stress.

Shoot lengths of grain sorghum and corn seedlings prior to, during and following exposure to water stress are presented in Tables 3 and 4, respectively. Shoot length was measured as an indicator of cell enlargement. In both species shoot length increased during the moderate stress treatment period, but at a much slower rate than in the control. A decrease in percent water content of 2.5 percent in corn (Figure 2B, page 20) and 4.5 percent in grain sorghum (Figure 1B, page 17) at the end of the six day moderate stress period resulted in large decreases in cell enlargement rates. During the severe stress treatment period, a decrease in percent water content of 5.5 percent in corn resulted in a cessation of cell enlargement as indicated by the lack of shoot elongation in Table 4. However, a decrease of 10 percent in percent water content in grain sorghum resulted in a severe reduction in cell elongation, but not a cessation (Table 3).

It appeared that smaller decreases in percent water content affected cell enlargement more in corn than in grain sorghum. Removal of both water

Table 3. Shoot length of stressed and nonstressed grain sorghum seedlings.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(cm)	
14[1]	18.7a[4]	18.5a	18.2a
17[2]	24.8a	22.3a	19.1b
20[3]	31.5a	26.7b	21.8c
24	38.0a	33.6a	27.8b
27	46.5a	38.1b	29.8c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

Table 4. Shoot length of stressed and nonstressed corn seedlings.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(cm)	
14[1]	38.6a[4]	38.2a	38.2a
17[2]	45.4a	39.5b	37.8b
20[3]	53.3a	44.7b	41.8c
24	61.0a	56.0b	51.7c
27	65.0a	59.5b	55.1c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

stress treatments in corn and grain sorghum resulted in a return of water content to normal with a corresponding increase in cell enlargement rates.

Protein Content

The protein content per plant of grain sorghum seedlings prior to, during and following exposure to water stress conditions is presented in Table 5. Protein content of the control seedlings increased continuously over the experimental period in a manner similar to increases in both fresh and dry weights (Figures 3 and 5, pages 22 and 26 respectively). The association of protein content per plant and dry weight per plant was found to be highly positively correlated (r = 0.96) when analyzed across all treatments and sampling dates. Protein content increased from approximately two mg to twelve mg per plant during the two week experimental period.

Six days of moderate stress did not significantly affect the protein content of the grain sorghum seedlings as the leaf water potentials of these plants gradually decreased (Table 1, page 16), but the protein contents were generally less than the control throughout the stress period. Three days of severe water stress reduced protein content 50 percent as the leaf water potential decreased 12 bars below that of the control seedlings. As did fresh and dry weights of sorghum seedlings, protein began to accumulate upon rewatering, but at a much slower rate, particularly in the severely stressed plants. After ten days of recovery from the three day severe stress treatment, reductions in protein content per plant were twice as much as the reductions resulting from the six-day moderate stress treatment with seven days of recovery.

Table 5. Protein content per plant of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	2.02a[4]	2.22a	2.02a
16	2.30a	2.02a	1.94a
17[2]	2.45a	2.26a	1.14b
20[3]	3.23a	3.25a	1.96b
24	7.06a	5.22a	2.38b
27	12.52a	7.91b	4.05c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

The protein content per unit dry weight of the nonstressed control and stressed grain sorghum seedlings is presented in Table 6. Protein concentration in the control seedlings tended to decrease throughout the experimental period as would be expected in plants exhibiting rapid dry weight increases with age. The moderate water stress treatment caused a slightly more rapid decline in protein concentration than in the control during the first three days of stress, however, after six days of stress the protein concentration was less, but not statistically different, than the control seedlings. Upon rewatering, the protein concentration of the moderately stressed seedlings continued to decline and was approximately 15 percent less than the nonstressed control at the end of the seven day recovery period. Three days of severe stress resulted in a sharp decline (32 percent) in the protein concentration of the sorghum seedlings as the leaf water potential decreased drastically. Upon rewatering and as the leaf water potential returned to normal, the decline in protein concentration continued but at a slower rate. At the end of the recovery period, reductions in protein content per unit weight were twice as much in the severely stressed seedlings as in the moderately stressed seedlings.

Protein content per plant of stressed and nonstressed corn seedlings is presented in Table 7. As with the grain sorghum seedlings, protein content per plant was highly positively correlated ($r = 0.89$) with dry weight. Reductions in protein content of corn seedlings, from exposure to moderate stress, were greater than in grain sorghum (Table 5) and ranged from 26 percent after three days to 30 percent after six days of stress. The protein content was 61 percent less than the control after exposure to three days of severe stress. Protein accumulations were faster in both

Table 6. Protein content per unit dry weight of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	53.48a[4]	53.33a	53.25a
16	51.47a	49.65b	47.84c
17[2]	46.52a	38.10b	31.55c
20[3]	43.28a	40.85a	32.24b
24	45.79a	40.27a	30.05b
27	43.40a	36.85b	29.09c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

Table 7. Protein content per plant of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	5.15a[4]	5.33a	5.18a
16	5.30a	5.29a	4.08b
17[2]	6.63a	4.76b	2.59c
20[3]	7.48a	5.20b	3.81c
24	9.66a	6.89b	4.67c
27	12.11a	8.84b	6.72c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

moderately and severely stressed plants upon rewatering than during each stress period. Reductions in protein content per plant were twice as severe in the severely stressed plants as in the moderately stressed at the end of both recovery periods.

Protein content per unit dry weight of nonstressed and stressed corn seedlings is presented in Table 8. The protein concentration of control seedlings tended to decrease with age during the experimental period as did the grain sorghum control seedlings (Table 6). As the leaf water potentials of the moderately stressed plants gradually decreased (Table 2, page 19), no significant differences in protein concentration were observed, except after three days of stress when the protein concentration was slightly less than the control. The effects of severe stress on the protein concentration of corn were very similar to grain sorghum during the stress period. After three days of severe stress, the protein concentration was 34 percent less than the corn control seedlings as compared to 32 percent in grain sorghum. The protein content per unit dry weight of the stressed corn seedlings returned to normal upon rewatering but did not in grain sorghum.

Both water stress treatments caused significant reductions in the protein content per plant of both corn and grain sorghum. Reductions were slightly more pronounced in corn during both stress periods especially in the severe, and were slightly more in sorghum at the end of the recovery periods. In both species three days of severe stress caused twice the reduction in protein content per plant as six days of moderate stress when measured at the end of the recovery period.

Table 8. Protein content per unit dry weight of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	32.50a[4]	33.93a	33.03a
16	29.76a	30.25a	27.35b
17[2]	29.04a	26.91b	19.03c
20[3]	24.42a	22.64ab	21.86b
24	21.75a	20.46a	20.64a
27	18.18a	18.02a	17.47a

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

RNA Content

The RNA content per plant of grain sorghum and corn seedlings prior to, during and following exposure to moisture stress conditions is shown in Tables 9 and 10, respectively. Total RNA accumulations per plant in the control seedlings of both species were highly correlated with the accumulation of protein per plant (Tables 5 and 7, pages 32 and 35 respectively). The correlation coefficients across all dates and treatments were r = 0.92 for grain sorghum and r = 0.86 for corn.

Moderate stress caused significant changes in the RNA content of sorghum seedlings only after six days exposure, however, at each sampling period the RNA content was slightly less than the control. Six days of moderate stress reduced the protein content of grain sorghum 26 percent. Unlike sorghum, moderate stress did cause significant reductions in RNA content of corn, beginning three days after the induction of the stress treatment. In both corn and sorghum, exposure to two days of severe stress caused no significant change in total RNA content. Three days of severe stress significantly reduced the RNA content of both species. These reductions were 37 percent in corn and 26 percent in sorghum.

Reductions in the RNA content of corn by severe stress throughout the stress and recovery period appeared to be slightly greater than reductions by moderate stress, although there was no statistical difference between the two treatments.

Severe stress caused a more pronounced reduction in the RNA content of grain sorghum during the 10 day recovery period than during the three day stress period. At the end of the recovery period, 27 days after planting, the moderate stress treatment resulted in a slightly greater

Table 9. Total RNA content per plant of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	0.24a[4]	0.27a	0.23a
16	0.32a	0.27a	0.25a
17[2]	0.35a	0.28a	0.26b
20[3]	0.53a	0.39b	0.35b
24	1.49a	1.14b	0.61c
27	1.95a	1.69a	1.19b

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

Table 10. Total RNA content per plant of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	1.16a[4]	1.00a	1.04a
16	1.84a	1.58a	1.53a
17[2]	2.22a	1.56b	1.40b
20[3]	2.96a	1.85b	1.60b
24	4.24a	3.24ab	2.24b
27	6.62a	4.60b	4.04b

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

reduction in RNA content per plant in corn than in sorghum, but no significant differences were found between species. Reductions caused by the severe stress treatment were the same for both species (approximately 38 percent) at the end of the recovery period.

Total RNA content per unit dry weight of nonstressed and stressed grain sorghum and corn is presented in Tables 11 and 12, respectively. Neither moderate nor severe stress treatments, both during and following each stress period, caused significant changes in the RNA concentration of corn and grain sorghum. However, three days of severe stress tended to increase the RNA concentration of both species. Large standard deviations, observed in the analyses of variance of these data possibly account for the lack of significant differences among treatments that have been reported in similar studies (50).

DNA Content

The DNA content per plant of grain sorghum and corn seedlings prior to, during and following exposure to water stress conditions is presented in Tables 13 and 14, respectively. The DNA content of the control seedlings for both species was found to increase with age. This increase in DNA content would be expected in rapidly growing plants that are accumulating dry matter. The correlations between DNA content per plant and dry weight, protein content and RNA content per plant were highly significant.

During the moderate stress and subsequent recovery period, increases in the DNA content of grain sorghum plants were generally slower than in the control, but no significant differences were found between

Table 11. Total RNA content per unit dry weight of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	8.54[4]	7.60	7.06
16	7.27	6.70	6.23
17[2]	6.58	4.75	7.95
20[3]	7.62	4.89	7.26
24	9.76	9.30	7.63
27	6.76	7.86	7.99

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Values within each date are not significantly different at the 0.05 level of probability.

Table 12. Total RNA content per unit dry weight of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	7.38[4]	6.78	6.77
16	10.29	9.16	10.20
17[2]	9.60	9.04	10.69
20[3]	9.40	8.20	9.17
24	9.59	9.44	10.12
27	9.90	9.41	10.68

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Values within each date are not significantly different at the 0.05 level of probability.

Table 13. DNA content per plant of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(μg)	
14[1]	15.9a[4]	14.4a	14.4a
16	18.6a	15.8a	16.7a
17[2]	25.5a	28.5a	17.1a
20[3]	33.9a	34.3a	25.4a
24	55.2a	52.8a	33.1b
27	99.3a	80.3a	48.8b

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

Table 14. DNA content per plant of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment Control	Moderate	Severe
		(µg)	
14[1]	75.2a[4]	70.5a	75.5a
16	82.2a	81.1a	67.6a
17[2]	97.1a	85.6a	55.8b
20[3]	138.1a	122.9a	86.1b
24	222.7a	185.9a	125.1b
27	347.8a	228.1b	172.5c

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Within each date, values followed by the same letter are not significantly different at the 0.05 level of probability.

the two treatments. The moderate stress treatment appeared to retard normal increases in DNA content of corn seedlings, particularly during the recovery period. The severe stress treatment caused a significant reduction in DNA content of corn and sorghum, especially during the recovery period. Three days of severe stress caused a 40 percent reduction in the DNA content of corn and approximately a 33 percent reduction on DNA content of grain sorghum. At the end of the severe stress recovery period, the DNA content of both species was approximately 50 percent of the control.

The DNA content per gram dry weight of grain sorghum (Table 15) and corn (Table 16) was not affected by either moisture stress treatment. These data indicate that the DNA concentration remained fairly constant and, therefore, moisture stress had presumably no effect on chromosomal multiplication. Although the DNA content per plant and per unit dry weight was higher in corn than in grain sorghum, changes in DNA content by the moisture stress treatments were the same in relation to the control seedlings.

Carbohydrates

Total sugar content per plant of grain sorghum and corn seedlings prior to, during and following exposure to moisture stress conditions is presented in Tables 17 and 18, respectively. The total sugar content of both nonstressed grain sorghum and corn seedlings increased as the dry weight of the plants increased (Figures 5 and 6, pages 26 and 27 respectively). The effects of moisture stress treatments in both corn and grain sorghum were inconsistent. However, in general, both moisture stress treatments retarded normal accumulation of total sugars in both species

Table 15. DNA content per unit dry weight of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(μg/g)	
14[1]	429[4]	346	393
16	427	391	416
17[2]	488	485	484
20[3]	491	434	496
24	363	408	411
27	311	373	359

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Values within each date are not significantly different at the 0.05 level of probability.

Table 16. DNA content per unit dry weight of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(μg/g)	
14[1]	463[4]	491	509
16	471	479	478
17[2]	506	473	449
20[3]	443	489	478
24	504	521	532
27	521	467	457

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

[4]Values within each date are not significantly different at the 0.05 level of probability.

Table 17. Total sugar content per plant of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	2.8	2.7	3.4
16	3.9	3.4	2.4
17[2]	4.3	5.0	4.2
20[3]	4.3	4.0	4.1
27	23.1	19.9	10.8

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 18. Total sugar content per plant of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	11.4	9.7	9.3
16	13.0	10.9	13.0
17[2]	15.9	16.4	9.4
20[3]	17.2	18.7	13.2
27	51.5	34.8	18.6

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

during the recovery period. The total sugar content per plant of corn was generally higher than in grain sorghum. This would be expected, since the dry weights of the corn seedlings were greater than grain sorghum. On a unit dry weight basis, no consistent response to water stress treatments was found in either grain sorghum (Table 19) or corn (Table 20). In general the total sugar content per unit dry weight of grain sorghum was greater than that of corn.

The total nonstructural carbohydrate content per plant of stressed and nonstressed grain sorghum and corn seedlings throughout the experimental period is presented in Tables 21 and 22, respectively. Total nonstructural carbohydrate content of the nonstressed control seedlings, like total sugar contents, increased throughout the experimental period. Both moisture stress treatments appeared to slow normal accumulations of total nonstructural carbohydrates during the recovery period in grain sorghum and corn. Three days of severe stress retarded normal accumulations in total nonstructural carbohydrate content more than did six days of moderate stress in both species. Throughout the experimental period, total nonstructural content per plant was greater in corn than in grain sorghum.

The total nonstructural carbohydrate content per unit dry weight of nonstressed and stressed grain sorghum and corn is given in Tables 23 and 24, respectively. Moisture stress treatments did not appear to alter the total nonstructural carbohydrate concentration of either species. The total nonstructural carbohydrate content per unit dry weight appeared to be slightly greater in the nonstressed grain sorghum seedlings than in corn.

Table 19. Total sugar content per unit dry weight of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	75.9	71.6	78.2
16	78.8	79.2	72.4
17[2]	78.4	99.7	103.0
20[3]	80.0	58.0	85.8
27	90.0	94.2	83.6

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 20. Total sugar content per unit dry weight of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	58.8	49.2	53.7
16	65.1	79.8	70.8
17[2]	60.4	87.1	62.3
20[3]	52.0	74.0	87.6
27	72.8	60.3	57.6

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 21. Total nonstructural carbohydrate content per plant of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment Control	Moderate	Severe
		(mg)	
14[1]	10.6	10.4	13.0
16	14.1	13.2	10.1
17[2]	16.0	15.8	11.8
20[3]	13.2	18.6	13.5
27	81.5	72.7	41.4

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 22. Total nonstructural carbohydrate content per plant of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg)	
14[1]	47.2	50.8	40.3
16	48.7	34.5	49.1
17[2]	62.9	50.0	36.6
20[3]	74.6	64.1	42.7
27	169.8	147.8	80.1

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 23. Total nonstructural carbohydrate content per unit dry weight of grain sorghum seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	285.9	279.6	297.2
16	283.8	304.2	304.4
17[2]	294.4	313.7	292.0
20[3]	313.0	268.0	283.8
27	318.0	344.2	321.6

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

Table 24. Total nonstructural carbohydrate content per unit dry weight of corn seedlings prior to, during and following exposure to moisture stress conditions.

Days After Planting	Moisture Stress Treatment		
	Control	Moderate	Severe
		(mg/g)	
14[1]	242.8	257.2	231.7
16	244.1	252.8	267.8
17[2]	239.4	266.1	241.3
20[3]	226.0	254.0	283.6
27	239.8	256.3	248.6

[1]Stress induced.

[2]Severe stress removed.

[3]Moderate stress removed.

The carbohydrate data presented in Tables 17-24 are results in which replications of treatments were bulked together in order to obtain a sample large enough for the analyses. Therefore, no statistical analyses were applied to these data.

CHAPTER V

DISCUSSION

Production of moisture stress on seedling roots with the osmoticum Carbowax 4000 and propagation of the plants in an environmentally controlled chamber allowed what was considered to be an adequate system for studying and comparing the effects of water stress on the two species. The design of this experiment was such that exact moisture stress conditions could be duplicated as closely as possible for each species. Preferably, both species would have been grown at the same time, but large differences in seedling growth rate prevented the use of such a design in a growth chamber. For example, two weeks after planting, the dry weights of corn seedlings were five times greater than grain sorghum seedlings of the same age. Differences in the transpiration rates of corn and sorghum were not apparent in the present study, since both species began to wilt in the same length of time following induction of moisture stress. The use of hydroponic growth media was assumed to remove any differences in water uptake due to differences in the extent of the root systems of these two species, and this was not considered to be a factor in this experiment.

Average leaf water potentials of the nonstressed corn seedlings throughout the experiment were approximately one bar lower than the nonstressed grain sorghum seedlings. Changes in leaf water potential, induced by the two moisture stress treatments, varied markedly. Grain sorghum seedlings subjected to both moderate and severe stress treatments exhibited greater reductions in leaf water potential than did corn.

Sanchez-Diaz and Kramer (36) also found that the leaf water potential of sorghum plants was lower than corn when subjected to equal periods of drying in a growth chamber.

The lower leaf water potentials that developed during water stress resulted in larger decreases in percent water content of grain sorghum than corn. In both species the correlation between leaf water potential and percent water content was highly significant ($r = 0.92$ and 0.94 for grain sorghum and corn, respectively).

Shoot length was measured as an indicator of cell enlargement. Data of Acevedo, Hsiao and Henderson (1) indicate a close dependence of cell enlargement on cell turgor. Smaller decreases in percent water content of corn resulted in greater reductions in cell enlargement than in grain sorghum during the water stress periods. Although the leaf water potential of grain sorghum was significantly lower than corn during the severe stress period and the percent water content was also lower, cell enlargement continued but at a very slow rate. This indicated that some cell turgor was retained in grain sorghum that allowed cell enlargement to continue during stress. Percent relative turgidity and its counterpart, water saturation deficit, were not measured in this study. However, possibly the water saturation deficit was less in grain sorghum than corn, since cell enlargement continued at lower leaf water potentials. Sanchez-Diaz and Kramer (36) reported that the water saturation deficits of grain sorghum were less than corn although the leaf water potentials of sorghum were lower. They considered this to be characteristic of drought resistant species.

Growth as measured by changes in dry weight during exposure to the moderate stress treatment was inhibited more in corn than in grain sorghum. A 2.5 bar reduction in leaf water potential below that of the nonstressed control resulted in a 30 percent reduction in the dry weight of corn. In contrast, a 5.6 bar reduction in leaf water potential of grain sorghum during the moderate stress period resulted in a 15 percent reduction in dry weight. These results indicated that during periods of rapid growth small reductions in leaf water potential resulted in a greater inhibition of growth in corn than in grain sorghum.

A similar trend was observed in seedlings subjected to severe stress conditions. At the end of the stress period, the leaf water potential of grain sorghum was 12 bars below the control and in corn only 6.3 bars below the control although the resulting dry weight reductions were the same in both species. Therefore, the reduction in dry weight per unit reduction in leaf water potential was less in sorghum than in corn.

Growth responses were slightly different in the two species upon rewatering but not statistically significant. The leaf water potentials of both corn and grain sorghum returned to normal upon rewatering, but the rates of dry matter accumulation did not. Dry matter accumulation during the recovery period appeared to be slightly faster in corn than in grain sorghum, although less than the control in both species. Moderate water stress resulted in no significant reductions in the dry weight of grain sorghum but the subsequent growth rate upon rewatering was slower than in the nonstressed control. The growth rate of moderately stressed corn increased upon rewatering and was similar to the growth rate of the control, especially during the latter part of the recovery period. The growth rate following removal of the severe stress treatment appeared to be slightly faster in corn than in sorghum, particularly towards the end of the recovery period but no statistical differences were found between the two species. In both species reductions in dry weights were greater after one week of recovery than at the time the severe stress treatment was removed. This lag in dry weight accumulation was possibly due to the slow rate of protein accumulation upon rewatering.

Growth rates have been reported to be closely associated with protein synthesis (51, 52). In this study the highly significant positive correlation between dry weight per plant and protein content per plant indicates that reductions in growth were most likely due to reductions in protein content. Protein accumulation in grain sorghum was not affected by moderate water stress, but during the same stress period protein accumulation in corn was reduced 30 percent. Upon removal of the moderate stress treatment, protein accumulation was slightly more rapid in corn than in grain sorghum, but no statistical differences were found between the two species.

Severe water stress conditions caused large reductions in the protein content of both corn and grain sorghum. Under severe stress conditions, no accumulations in protein were apparent since the protein content per plant was lower at the end of the stress period than prior to imposing the stress. The protein content of both species was slightly less than 50 percent of that in the seedlings prior to moisture stress induction. As the leaf water potentials of both species returned to normal during the recovery period, protein accumulations occurred at a faster rate in corn than in grain sorghum.

Protein content on a per plant basis appeared to reflect changes in the dry weight of the seedlings. On a unit dry weight basis, protein concentration was affected slightly more by moderate water stress in corn than in grain sorghum, particularly during the recovery period. The protein concentration of severely stressed corn quickly returned to values similar to the nonstressed control upon rewatering. In contrast, the protein concentration of grain sorghum during recovery from severe stress remained approximately 33 percent lower than the nonstressed control.

Grain sorghum seedlings appeared to have the ability to accumulate dry matter upon recovery from severe water stress even though the protein content per unit dry matter was much lower than that of the nonstressed control. Dry matter accumulations in corn seedlings during recovery from severe stress appeared to be the same in relation to the control as was dry matter accumulation in grain sorghum, however, the protein content per unit dry weight was the same as that of the control in corn and not in grain sorghum.

Reductions in protein content during periods of water stress have been observed in similar studies with corn (42, 48, 49, 51) and with other plant species (2, 4, 17, 18, 41). These reductions were attributed to either decreased protein synthesis, increased protein degradation or both.

Grain sorghum seedlings were found to have a higher percentage of protein than corn seedlings throughout the experimental period. During the experimental period the percent protein of the control seedlings appeared to decrease faster in corn than in grain sorghum. This was possibly due to a dilution effect, since the corn plants were much larger than the sorghum plants. Reductions in net accumulations of RNA content per plant by both water stress treatments closely paralleled reductions in total dry weights of the seedlings as indicated by the highly significant correlation between these two parameters. This association of RNA with growth rate agrees with similar studies on corn roots (51, 52). The RNA contents per unit dry weight were not significantly altered by either water stress treatment in both species. These results indicate that the protein-synthesizing machinery of both corn and grain sorghum did not undergo any considerable alteration during water stress.

The lack of significant differences in total RNA content per unit dry weight in both corn and grain sorghum, during periods of water stress and subsequent recovery, indicates that changes in protein content were not a result of changes in RNA content. However, changes in various RNA forms were not measured in analysis of total RNA content. Protein synthesis is dependent upon ribosomal, messenger and transfer RNA. Changes in any one or more of these RNA fractions could cause reductions in protein synthesis. Therefore, only correlative evidence exists between changes in total RNA content and protein content.

West (49) observed that the RNA content per stem section and per cell of six day old corn seedlings increased under water stress conditions. No significant changes in RNA content per unit dry weight of the entire shoot of corn were observed in the present study.

Significant differences observed in DNA content per plant of both corn and grain sorghum during and following water stress conditions appeared to reflect differences in dry weights, since no differences in DNA content per unit dry weight were observed. Rates of change in quantities of DNA and in dry weight per plant were highly correlated ($r = 0.99$ for grain sorghum and 0.97 for corn). The DNA content per plant increased throughout the experiment, thus it appears that chromosomal multiplication was not affected in either species by moisture stress.

A close association exists between RNA content and DNA levels (51, 52). From the standpoint of RNA translation from DNA, adequate levels of DNA appeared to be present for RNA translation. However, changes in RNA could have occurred and retarded protein synthesis in ways that were not detectable by analysis of total RNA content.

Total sugar content per plant of both corn and grain sorghum increased throughout the experimental period. This increase in total sugar content would be expected in plants that are accumulating dry matter. The effects of moisture stress on total sugar contents of both species were inconsistent during the stress periods, however, during the recovery periods reductions in total sugar content were apparent. The total sugar content per plant appeared to be slightly higher in corn than in grain sorghum. Maranville and Paulsen (28) observed that fructose, glucose, and sucrose concentrations of corn seedlings were not significantly affected by either medium or severe moisture stress. Total sugar content per unit dry weight was not affected by either stress treatment in either corn or grain sorghum. Total sugars appeared to account for a larger portion of the total dry weight of grain sorghum than corn. Possibly this could account for the lower leaf water potentials observed in grain sorghum during the stress periods than in corn. This is based on the assumption that larger amounts of total sugars in grain sorghum would cause the osmotic potential of the cells to be lower (more negative). In plant cells that are less than fully turgid, osmotic potential accounts for a large portion of the total water potential of the cell (23).

Total nonstructural carbohydrate content per plant of corn and grain sorghum increased throughout the experimental period in a manner similar to total sugar content. Total nonstructural carbohydrate content per unit dry weight was not affected by either water stress treatment in corn or grain sorghum.

Correlations between total nonstructural carbohydrate content per plant and dry weight, and between total sugar content per plant and dry weight were found to be highly significant.

In general, grain sorghum seedlings appeared to have no advantage over corn seedlings in response to water stress. Although dry matter accumulation during the moderate stress period was not significantly reduced in sorghum and was significantly reduced in corn, growth during the recovery period was the same in both species. The growth rate appeared to be slightly faster in corn than in sorghum, particularly at the end of the recovery period. During and following exposure to severe stress, changes in dry weight were the same in both species. As during recovery from moderate stress, the growth rate during the severe stress recovery period appeared to be slightly faster in corn than in sorghum. Investigation of growth responses for longer periods of recovery would have been of interest, but the hydroponic system utilized in the study was not capable of supporting plants much older than four weeks. Possibly, corn might have recovered from this water stress better than sorghum.

Removal of possible advantages in root development of grain sorghum and the maintenance of high humidities in the growth chamber appeared to suppress any large differences in the drought resistance of these two species. Changes in the water status of grain sorghum seedlings were similar to those reported by Sanchez-Diaz and Kramer (36) as being characteristic of a drought resistant species. The leaf water potential of grain sorghum was reduced more than in corn without any deleterious effects on growth. Cell turgor appeared to remain higher in sorghum than corn although the leaf water potentials of sorghum were lower. The lower leaf water potentials of stressed grain sorghum seedlings could be due to the larger total sugar concentrations that were found in the seedlings.

The major biochemical difference observed between the two species in response to water stress was the lower protein content per unit dry weight of grain sorghum during recovery from severe stress. Under the conditions of this experiment, the low protein concentration of sorghum may have been a disadvantage to superior drought resistance rather than an advantage.

Although grain sorghum is more drought resistant, as indicated by its major region of production, both corn and grain sorghum respond readily to irrigation even when moisture conditions appear to be adequate (5). In regions that are favorable for both corn and grain sorghum, corn is generally preferred to grain sorghum. Corn plants can withstand periods of mild water stress and recover upon rewatering and produce higher yields than grain sorghum. Grain sorghum plants, however, can withstand periods of drought that are severe enough to cause permanent wilting of the leaves. Sorghum plants have the ability to produce regrowth by tillering following exposure to extremely severe drought whereas corn plants do not possess this ability to tiller.

CHAPTER VI

SUMMARY

Grain sorghum and corn seedlings were grown in hydroponic growth media in an environmentally controlled chamber for two weeks under optimum conditions. Water availability to the plant roots was then reduced by increasing the osmotic potential of the nutrient solutions with polyethylene glycol of approximately 4000 molecular weight. Plants were subjected to either three days of severe (-10 bars) or six days of moderate (-5 bars) water stress and then rewatered. A nonstressed control treatment was maintained throughout the experimental period. Leaf water potentials were measured prior to each harvest of shoot samples throughout the experiment. Shoot length and weight and protein, nucleic acid and carbohydrate content were determined prior to, during and following exposure to moisture stress conditions.

The average leaf water potentials of nonstressed corn and grain sorghum were approximately the same throughout the experiment. Leaf water potentials were lower in grain sorghum than corn during both water stress periods. Percent water content was less in grain sorghum than corn during the water stress periods. Smaller decreases in percent water content resulted in greater reductions in cell enlargement in corn than in sorghum during the stress periods. Apparently, cell turgor was maintained at lower leaf water potentials in sorghum than in corn. Upon rewatering, the leaf water potentials and percent water content returned to normal in both species. The correlations between leaf water potential and percent water content of both corn and sorghum were highly significant.

Dry matter accumulations were significantly retarded by the moderate stress treatment in corn but not in sorghum. Upon rewatering, rates of dry matter accumulation in corn returned to normal. Severe stress conditions resulted in large reductions in dry matter accumulation rates of both species. Percent reductions in dry matter accumulation during recovery from severe stress became progressively more pronounced, since the growth rate of the nonstressed control seedlings was much greater than in the stressed seedlings. In both species reductions in dry weight were twice as severe in the plants subjected to three days of severe stress as those in the plants subjected to six days of moderate stress.

Protein accumulations in grain sorghum on a per plant basis were not affected during the moderate stress period, but were significantly reduced during the recovery period. In contrast, moderate stress caused significant reductions in protein content of corn seedlings both during and following the stress period. On a unit dry weight basis, protein concentrations were initially reduced more in grain sorghum than in corn during the moderate stress period. Upon rewatering, the protein concentration of both species returned to normal. During the severe stress period, protein content per plant was reduced more in corn than in sorghum, but on a unit dry weight basis decreases in protein content were the same in both species. Upon removal of the severe stress treatment, protein content per unit dry weight returned to normal in corn but not in grain sorghum. Sorghum plants appeared to retain the ability to accumulate dry matter as did corn following exposure to severe water stress, although its protein content per unit dry weight was significantly lower than corn's.

The correlation coefficients between dry weight and protein content per plant were highly significant when calculated for all treatments and sampling periods.

Total RNA and DNA contents on a per plant basis were reduced approximately the same in both species throughout the experiment. The correlation coefficients between RNA and DNA contents per plant and dry weight were highly significant across all treatments and sampling periods. On a unit dry weight basis, total RNA and DNA contents were not affected by either moisture stress treatment during and following exposure to moisture stress. Thus, the protein-synthesizing machinery was not affected by water stress. Reductions in protein content and thus dry weight could not be attributed to decreases in total RNA content or DNA content.

Total sugar and total nonstructural carbohydrate content per plant was reduced following exposure to moisture stress. Total sugar and total nonstructural carbohydrate contents per unit dry weight were not affected by either moisture stress treatment in corn or grain sorghum. Both total sugar content per plant and total nonstructural carbohydrate content per plant were highly correlated with dry weight in both corn and grain sorghum.

From this study it appears that physiological responses of grain sorghum to water stress conditions were characteristic of drought resistant plants, since it was capable of withstanding larger decreases in leaf water potential than corn. Growth responses following exposure to water stress conditions were the same in both species. Total RNA and DNA concentrations were not affected by water stress conditions in either species, but protein concentration was affected more in grain sorghum than corn during recovery from severe stress. It appears that there were no major biochemical differences measured between corn and grain sorghum seedlings in response to water stress that would explain sorghum's greater ability than corn's to resist drought under natural conditions.

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APPENDIX

Table 25. Correlation coefficients between selected growth and physiological characters of corn and grain sorghum seedlings across all stress treatments and sampling periods.

Characters Correlated	Correlation Coefficients	
	Grain Sorghum	Corn
Leaf Water Potential-Percent Water Content	0.92**	0.94**
-Fresh Weight	-0.42**	-0.41**
-Dry Weight	-0.37**	-0.32**
Fresh Weight - Dry Weight	0.99**	0.99**
Dry Weight-mg Protein/Plant	0.96**	0.89**
-mg Protein/g Dry Weight	-0.24	-0.60**
-mg RNA/Plant	0.96**	0.93**
-mg RNA/g Dry Weight	0.03	0.14
-μg DNA/Plant	0.99**	0.97**
-μg DNA/g Dry Weight	0.59**	0.21
mg Protein/Plant-mg Protein/g Dry Weight	-0.07	-0.29*
-mg RNA/Plant	0.92**	0.86**
-mg RNA/g Dry Weight	0.11	0.02
-μg DNA/Plant	0.96**	0.95**
-μg DNA/g Dry Weight	0.63**	0.24
mg Protein/g Dry Weight-mg RNA/Plant	-0.28*	-0.62**
-mg RNA/g Dry Weight	-0.05	-0.35**
-μg DNA/Plant	0.70**	0.78**
-μg DNA/g Dry Weight	0.33*	0.66**
mg RNA/Plant-mg RNA/g Dry Weight	0.33*	0.37*
-μg DNA/Plant	0.96**	0.98**
-μg DNA/g Dry Weight	0.63**	0.26
mg RNA/g Dry Weight-μg DNA/Plant	0.20	0.64**
-μg DNA/g Dry Weight	0.29*	0.07
μg DNA/Plant-μg DNA/g Dry Weight	0.53**	0.35*
Dry Weight-mg Total Nonstructural Carbohydrates/Plant	0.99**	0.99**
-mg Total Nonstructural Carbohydrates/g Dry Weight	0.65*	0.23
-mg Total Sugars/Plant	0.99**	0.97**
-mg Total Sugars/g Dry Weight	0.33	0.12

*Significant at 0.05 level of probability.

**Significant at 0.01 level of probability.

Table 26. Comparisons of changes in growth and physiological parameters of corn versus grain sorghum in relation to the controls during moderate and severe stress periods and their respective recovery periods.

	Days After Planting			
	Moderate Stress		Severe Stress	
Parameters Compared	14-20	24-27	14-17	20-27
Reduction in Fresh Weight/Plant	ns[1]	ns	ns	ns
Reduction in Dry Weight/Plant	*	ns	ns	ns
Reduction in Protein Content/Plant	*	ns	*	ns
Reduction in Protein Content/Unit Dry Weight	*	ns	ns	*
Reduction in RNA Content/Plant	ns	ns	ns	ns
Reduction in RNA Content/Unit Dry Weight	ns	ns	ns	ns
Reduction in DNA Content/Plant	ns	ns	ns	ns
Reduction in DNA Content/Unit Dry Weight	ns	ns	ns	ns

[1]ns = Values not significantly different at the 0.05 level of probability.

*Values significantly different at the 0.05 level of probability.

VITA

William Keith Wesley was born in Griffin, Georgia, on October 24, 1946. He attended elementary and junior high school in Griffin, Georgia. He graduated from Griffin High School in June, 1964. The following September he entered Abraham Baldwin Agricultural College in Tifton, Georgia, and in June, 1967, he received an Associate in Science degree. In March, 1967, he entered the University of Georgia, and in June, 1969, received the Bachelor of Science degree in Agriculture. In March, 1969, he accepted a research assistantship at the University of Georgia and began study toward a Master's degree. In August, 1970, he received the Master of Science degree with a major in Agronomy.

He entered the Graduate School at the University of Tennessee in September, 1970, and received the Doctor of Philosophy degree with a major in Plant and Soil Science in December, 1973. He is a member of the American Society of Agronomy, Crop Science Society of America, Sigma Xi, Gamma Sigma Delta, and Phi Kappa Phi.

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