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**Effect of soil moisture stress on photosynthesis and other  
physiological characteristics of seven sorghum cytoplasms**

El-Majbari, Farag Ali Mustafa, M.S.

The University of Arizona, 1989

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EFFECT OF SOIL MOISTURE STRESS ON PHOTOSYNTHESIS AND OTHER  
PHYSIOLOGICAL CHARACTERISTICS OF SEVEN SORGHUM CYTOPLASMS

by

Farag Ali Mustafa El-Majbari

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A Thesis Submitted to the Faculty of the  
DEPARTMENT OF PLANT SCIENCES  
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For the Degree of  
MASTER OF SCIENCE  
WITH A MAJOR IN AGRONOMY AND PLANT GENETICS  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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## ABSTRACT

The experiment was conducted at the University of Arizona Campus Agricultural Center to evaluate the effect of soil moisture stress on photosynthesis, transpiration, diffusive resistance, temperature differential, leaf temperature, and specific leaf weight of seven sorghum Sorghum bicolor (L.) Moench cytoplasms represented by nine lines.

As soil moisture stress increased, diffusive resistance and leaf temperature increased whereas photosynthesis and transpiration decreased.

Temperature differential was highest under high soil moisture stress and lowest under medium soil moisture stress. Specific leaf weight was highest under medium soil moisture stress.

Three lines, AKS37, AKS38, and A<sub>2</sub>Tx398, representing two different germplasms under high soil moisture stress exhibited high photosynthesis and transpiration rates, high specific leaf weights, and low diffusive resistance.

Differences in photosynthesis rates under non-soil moisture stress between A<sub>1</sub> and A<sub>2</sub> cytoplasmic sterility systems were significant.

## INTRODUCTION

Water is the main requirement to sustain life for nearly all living plants and animals. The problem of drought or insufficient water for plants varies from area to area in the world, depending on the amount of rainfall and its variability in when it is received relative to the growing season. Unfortunately, most of the drought-affected areas have limited available sources of supplemental irrigation water, which makes it difficult for crop production to be fully successful. The development and use of drought-tolerant crops that use less water or use it more efficiently are ways of improving production under limited water resources. Plant genotypes with more water-efficient photosynthesis processes are one type of plant drought tolerance. Plants with greater drought resistance may be developed from genotypes showing greater photosynthesis efficiency under heat and soil moisture stress.

Sorghum is one of the most important inherently drought tolerant cereal crops in the world being used for human food and animal feed. In addition, in some areas, the stems are used as building material, and the plant remains, including roots, are used as fuel (House, 1979).

When compared to rice, wheat, and maize, sorghum also has a high yield potential under non-stress conditions (House, 1979). Sorghum as a C4 plant under soil moisture stress, is also one of the highly efficient plant species in photosynthesis and water use efficiency compared with other major cereal crops. Sorghum is a crop of choice to be grown under hot and dry conditions because of its better adaptation to this stressful type of environment compared to other crops grown for similar purposes. Sorghum has a more extensive and fibrous root system, compared to corn, which extracts a greater amount of moisture from a similar volume of soil (House, 1979). Therefore, sorghum does not require as much supplemental soil moisture as other cereal crops for comparable amounts of growth, development, and yield. Sorghum has the ability to suspend growth and development during a dry period then resume growth with the relief of soil moisture stress. Sorghum is also more likely to make grain even though temperatures are high, but it is not as tolerant of cool temperatures as corn (House, 1979).

Major processes of photosynthesis in plants is considered to occur in the cytoplasm of plant cells. In sorghum, the cytoplasm constituents, such as the chloroplasts, are maternally inherited. Ross and Hackerott (1972) inserted a common genome into six different cytoplasm. The purpose of this research is to compare the effect of soil moisture stress

on some physiological processes such as photosynthesis and other related physiological parameters in seven different sorghum cytoplasms.

## LITERATURE REVIEW

### Cytoplasmic Sterility

Production of sorghum hybrids using cytoplasmic male sterility that resulted from the interaction of milo cytoplasm and kafir chromosomal factors was discovered by the Texas Agricultural Experimental Station and the U. S. Department of Agriculture (Stephens and Holland, 1954). Ross (1965) emphasized that this was the starting point of obtaining high grain yield sorghum. York et al. (1974) reported that grain yields per unit area was remarkably increased from the time that cytoplasmic male sterility and fertility restoration was discovered. Today, most of the grain sorghum, Sorghum bicolor (L.) Moench, grown in the United States, and throughout the world, basically depends on one cytoplasmic-genic sterility combination. The milo cytoplasm is most dominant among all sorghum female parents (Schertz and Ritchey, 1978). The vulnerability caused by the use of a single cytoplasmic-genic-male sterility system for producing hybrids was dramatically illustrated in corn. In 1970 a southern corn leaf blight attacked the corn crop over all of the corn production area of the United States. The estimated yield reduction was 15% nationwide and 50% or more in some southern states (Horsfall, 1972). That corn crop hazard

brought the attention of researchers to look for other alternative cytoplasms to the existing system in sorghum. This situation is more critical in sorghum which has perfect florets, than in maize which is easy to detassel. Therefore, studies were begun to find new cytoplasmic-genic sterility systems in sorghum (Schertz, 1973). Based on previous research on sorghum male sterility, different sorghum cytoplasm genetic types were divided into groups or classes such as  $A_1$  and  $A_2$ . The first cytoplasmic sterility system in milo, now called  $A_1$ , was discovered by Stephens and Holland in 1954 (Quinby, 1980). The  $A_2$  cytoplasm was released by Schertz in 1976 (Schertz et al., 1981). The difference between  $A_1$  and  $A_2$  cytoplasmic sterility systems was that  $A_1$  fertility restorer lines for F1 hybrid also maintained  $A_2$  sterility. This means both sorghum cytoplasmic sterilities have the same male sterility inducing system but the  $A_2$  restoration is different because of modifying genes (Worstell et al., 1984). Then they found that by crossing the same male parents with  $A_1$  and  $A_2$  female parents, the hybrids with class " $A_1$ " sterility system had less fertility than the hybrids with class " $A_2$ " sterility system. This indicated that the differences in fertility between the two classes of cytoplasmic sterility systems,  $A_1$  and  $A_2$ , are related to the degree of fertility restoration. Schertz (1977) also reported that the  $A_2$  cytoplasmic sterility system was different

from the A<sub>1</sub> cytoplasmic sterility system in sterility response.

Cytoplasm grouping based on fertility restoration was supported by restriction endonuclease analysis (Pring et al., 1982). Pring et al. (1981) also mentioned that the mitochondrial and chloroplast DNA's of milo cytoplasm was different from kafir cytoplasm. They also found that the mitochondrial DNA of "A<sub>2</sub>" cytoplasm was differentiated from the "A<sub>1</sub>" cytoplasm. According to mitochondrial and chloroplast DNA comparisons, sorghum male-sterile cytoplasms were classified into eight groups (Pring et al., 1982). An analysis of mitochondrial DNA of KS34 to KS39 showed that KS34, 38 and 39 belong to the milo cytoplasm class and KS35, 36 and 37 differ from milo cytoplasm class, but the chloroplast DNA did not show any differences (Conde et al., 1982).

#### Photosynthesis and Its Related Physiological Aspects

The fact that photosynthesis occurs in chloroplasts is documented in many studies of higher plants. The chloroplast is the site of the essential apparatus where photosynthesis takes place. The chloroplasts are located in the cytoplasm of the plant cell (Sestak et al., 1985; Gardener et al., 1985; Noggle and Fritz, 1983; Ting, 1982; Raven et al., 1981). The cytoplasm does not transfer from the male parent to the offspring during fertilization of the

female egg cell. Elseth and Baumgardner (1984) stated that chloroplasts are inherited from one generation to another only through the female parent egg without any contribution from the male parent pollen. Hence, the differences in photosynthesis from one cytoplasm to another are due to the differences in cytoplasm sources. It follows that results of studies of the behavior of photosynthesis under different environmental conditions are actually indications of the behavior of cytoplasms as determined by the chloroplasts within the cytoplasms.

Photosynthesis is a plant mechanism easily affected by environmental factors such as temperature and light. It is also affected by soil moisture stress which affects the stomatal response and root system function. Photosynthesis is one of the major factors affecting yield. Gardner et al. (1985) reported that photosynthesis is the basis of crop production and the amount of yield ultimately depends on the size and efficiency of the photosynthetic system. The photosynthetic system is regulated by nuclear and chloroplast genes (Miles and Metz, 1985). Heichel and Musgrave (1969) stated that the vigor of leaf maize photosynthetic activity varied according to hybrid cross combination differences. In addition, variation in the activity of photosynthesis of a maize leaf may be related to growth stage differences at the time of measurement of photosynthesis (Sinha and Khanna,

1975). Alfalfa cultivars with greater total leaf area and higher total photosynthetic rate per plant produced the greatest forage yield (Leavitt et al., 1979).

Photosynthesis relates differently to different physiological characters. According to Akita et al. (1986), the rate of photosynthesis was highly correlated to transpiration rate. Bryanl et al. (1895) reported that the relationship between increasing photosynthesis and stomatal conductance in johnsongrass (Sorghum halepense) was in the shape of a curve. They concluded that stomatal opening was very much affected by rising leaf temperatures and decreasing water potential. Photosynthesis may be negatively affected by increasing osmotic concentrations which in turn decreases as relative moisture content percent increases. The rate of photosynthesis declines with increases or decreases in air temperature beyond the optimum range, which varies with species and ecotypes. Hence, the optimum temperature range for C<sub>4</sub> crops is from 30 to 45°C and net photosynthesis is from 1.5 to 2.5 mg m<sup>-2</sup>s<sup>-1</sup> when the other factors are generally optimum (Berry and Raison, 1981). Markes and Taylor (1978) stated that the optimum temperature for photosynthesis in leaf changes according to its age. The temperature optimum of net photosynthesis in young mature leaves is high and decreases as the leaf gets older. Brynal et al. (1985) observed that the water lost by transpiration and the diffu-

sion of CO<sub>2</sub> into a johnsongrass plant leaf was regulated by stomatal conductance, which was affected by increases in both leaf moisture stress and leaf temperature. Catsky et al. (1985) stated that it is difficult to determine whether the variation in stomatal conductance is due to plant ontogeny or due to changes in immediate environmental conditions such as air temperature because stomatal conductance is affected by environmental changes during the days preceding the measurement. Orozco et al. (1983) reported that leaf conductance increased as water potential increased. Hence, leaf conductance is positively associated with moisture availability. Stomatal conductance reaches the peak in mature or semi-matured leaves and declines throughout senescence of the leaf. On a daily basis, stomatal conductance is higher in new leaves and lower in old leaves (Catsky et al., 1985). A decline in moisture potential prevented the development of plant parts, but this suppression of development was not the same in all parts of a single plant (Westgate and Boyer, 1985). Skre et al. (1983) pointed out that moisture content of a leaf is an important factor limiting moss plant photosynthesis under field conditions.

Photosynthesis may also be related to specific leaf weight. According to several previous studies, there was a high correlation between SLW and photosynthesis (Kerby et al., 1980; Marini and Marini, 1983; Jurik, 1985; Oren et al.,

1986; Wooge and Barden, 1987). On the other hand, Akita et al. (1986) stated that the correlation between photosynthetic rate and SLW was very weak. Karami and Weaver (1980) pointed out that the relation between photosynthetic rate and SLW in cotton leaves was not positively significant. Plant species may have the same SLW but produce photosynthate differently because of genetic and environmental influences on leaf physiology and leaf structure which do not always affect photosynthetic activity (Jurik, 1986).

The relationship of SLW with photosynthesis and respiration is essential. SLW is a plant measurement tool that makes the plant able to maintain leaf mass which is necessary for continuity of the ratios of photosynthesis, respiration and plant development (Murei and Shul'gin, 1978). Wooge and Barden (1987) stated that SLW was highly correlated with leaf thickness and palisade depth. SLW could be utilized in morphological and physiological leaf descriptions such as leaf net photosynthetic potential. According to Ghosh (1973), there was a correlation between thick leaves having thick palisade tissue and high photosynthetic rates. Marini and Barden (1981) pointed out that rate of photosynthesis declined close to the end of the growing season but SLW remained high throughout the season. For this reason, their linear relationship became poor. Hence, SLW may furnish a rational index of net photosynthesis in the beginning

of the season when the leaves are young but not at the end of the season because of the decline in the rate of photosynthesis at that time. Jurik (1986) reported that SLW may be used for photosynthesis measurement. Carlson et al. (1981) stated that because of the positive relationship between SLW and photosynthesis, SLW may be utilized as a selection criterion for forage production. They also found that in grass plants, high seed yield per plant is a result of large panicles, which are correlated with high SLW. Dornhoff and Shibles (1970) mentioned that because of the correlation of SLW with the rate of photosynthesis, SLW may serve as an index for breeding selection. Palit and Bhattacharyya (1984) suggested that leaf area and leaf area index of jute plant (Corchorus capsularis L. and C. olitorius L.) at any stage could be calculated by dividing its leaf dry weight by its average SLW values. In earlier work, Palit and Bhattacharyya (1979, 1980) documented that the lower leaves in a plant had less average SLW than the upper leaves because the younger and higher leaves received more light and produced more photosynthate more efficiently than the older leaves.

Crop yield is not only related to photosynthetic rate but also to how the photosynthate is translocated and utilized by the plant (Kuo et al., 1980). They added that cultivar differences in leaf net photosynthesis could be

associated with improvement of crop yield. For example, they found that in mung bean, high seed yield might be related to high photosynthetic rate which may be obtained by selecting genotypes which have high SLW, high harvest index, and an increased RUDPcase (enzyme) activity. During pod filling in soybean, canopy apparent photosynthesis was highly correlated with grain yield (Harrison et al., 1979).

Specific leaf weight was found to be genetically controlled (McGee et al., 1981; Ledig and Korbolo, 1983) and environmentally controlled (Jurik et al., 1979). Environmental effects were found to have a greater influence on SLW than genetic effects (Jurik, 1986). In different studies of tall fescue (Festuca arundinacea Schreb.), Nelson et al. (1978) found that SLW was affected by temperature. Then Wolf et al. (1979) found that radiation density was affecting it too, as was moisture content (Silcock and Wilson, 1982). MacAdam and Nelson (1987) found that low temperature increased water-soluble carbohydrate, which is a component of SLW. The components that contribute to SLW are water soluble carbohydrate, starch, organic acids, and proteins. SLW is also affected by other factors such as structural and nonstructural carbohydrate and cell size and number (Marini and Barden, 1981). Ostman and Weaver (1982) stated that retranslocation of sugars and nutrients reduces SLW during the senescence period in apple trees.

Direct and Indirect Effects of  
Moisture Stress on Photosynthesis  
and Other Parameters Studied

Moisture stress showed a great effect on leaf water potential, photosynthesis and leaf conductance relationships (Jones and Rawson, 1979). The main factor controlling stomatal opening was leaf water potential, but at the same time photosynthesis may be indirectly controlled by the increase of internal CO<sub>2</sub> concentration which in turn influences stomatal conductance (Farquhar and Sharkey, 1982). If crop plants are well irrigated, transpiration will be at an optimum rate so that plants remain relatively cool. But if crop plants are under moisture stress, transpiration will be reduced and plant temperature will rise, leading to a reduction in photosynthesis (Idso et al., 1981). Fukushima et al. (1985) stated that photosynthesis activity was directly affected by changes in leaf moisture balance which resulted from the impact of soil moisture stress. They concluded that as soil water decreased, rate of photosynthesis decreased, along with a decline of transpiration, leaf water content, leaf water potential, and an increase in diffusive resistance. They also concluded that photosynthesis and transpiration were positively correlated. O'Toole and Moya (1978) stated that degree of rolling and leaf water potential were highly correlated in rice plants under high water stress. O'Toole and Cruz (1980) pointed out that the

relationship between leaf water potential and leaf diffusive resistance was linear. The activity of photosynthesis was reduced by increasing osmotic stress and also light efficiency declined under moisture stress (Mougou et al., 1983). Leach (1980) observed, from field enclosure and chamber measurements, that there was little or no effect from water stress on carbon dioxide assimilation per unit of leaf area of barley (Hordeum vulgare L.) He also observed that the net photosynthesis rates per unit leaf area of single leaves of barley showed no reliance on water stress. Parkinson and Day (1983) observed that there was no clear effect of water stress on quantum yield. Huber et al. (1984) observed that the carbon exchange rate (CER) was reduced as soil moisture stress increased, but the CER reduction was not just a function of stomatal closure because intercellular CO<sub>2</sub> concentration was not extensively decreased compared with well-watered plant leaves. Bunce (1982) reported that a decline in both stomatal and mesophyll conductance, due to the effect of water stress, reduced photosynthetic rate in the leaves of soybean and sunflower almost three-fold and all of the net photosynthetic rates and stomatal and mesophyll conductances were reduced under the water stress conditions. His findings agreed with those of Huber et al. (1984) that photosynthesis reduction was not just related to stomatal closure. Munger et al. (1987) reported that the rate of

photosynthesis increased with stomatal conductance to a level of  $1.5 \text{ cm s}^{-1}$  but above that point there was no increase in rate of photosynthesis. This suggested that non-stomatal restrictions to rate of photosynthesis such as  $\text{CO}_2$  flux into the leaf and water loss due to respiration were directed by stomatal conductance and non-stomatal influences such as soil moisture and atmospheric factors.

A soil moisture deficit, besides its effect on photosynthesis activity and stomatal conductance, also has effects on other physiological aspects such as leaf temperature, temperature differential, transpiration and specific leaf weight.

The canopy temperatures of sorghum under water stress was higher than under well-irrigated plants (Chaudhuri and Kanemasu, 1982). This is supported by Kannangara et al. (1983), who observed that leaf diffusive resistance and leaf temperature were elevated by soil moisture stress. Millard et al. (1978) had previously mentioned that leaf and canopy temperatures were associated with the moisture stress in the plant. Clarke and McCaig (1982b) also found that as moisture stress increased, diffusive resistance increased and leaf temperature became close to ambient temperature in rape plants (Brassica campestris and B. napus).

Diffusive resistance was found to be associated with moisture stress (Kannangara et al., 1983; Clarke and McCaig,

1982b) and temperature differential was correlated to stomatal conductance (Kadoya, 1978). Therefore, temperature differential can be considered to be affected by water stress.

The transpiration rate declined significantly and leaf temperature increased at high soil moisture stress (Miura, 1982). Ibrahim et al. (1985) also observed in pearl millet (Pennisetum americanum [L.] Leeke) that transpiration was reduced and diffusive resistance was increased under soil moisture stress. It has been observed that diffusive resistance increased and leaf water content decreased as soil moisture stress increased (Bansal and Nagarajan, 1986; Chaudhuri and Kanemasu, 1982). Plant water use efficiency was found to be reduced by moisture stress, but the reductions became less when the soil moisture stress increased gradually during the growing period (Dennis et al., 1982). This suggests high moisture stress control through osmotic adjustment of leaves of many plants (Fererres et al., 1978; Jones and Turner, 1978; Jones and Rawson, 1979; Morgan, 1980).

Water stress increased specific leaf weight (SLW) in C<sub>4</sub> grasses and rewatering decreased it; but in soybean, SLW tended to increase throughout the drought period and also during the recovery period (Patterson, 1986). The conclusion can be that soil moisture stress increases SLW because during the leaf expansion period water stress reduces cell sizes

which, in turn, results in a small leaf area occupied by the same mass of cells (Smith and Nobel, 1978). Leaf area is more sensitive to moisture stress than is stem elongation (Kannangara et al., 1983). Therefore, SLW is observed to increase under water stress condition because SLW is equal to leaf dry weight divided by the leaf area. Plant height, dry matter and leaf area index were observed to be linearly related to moisture level (Chaudhuri and Kanemasu, 1982). Gregory and Squire (1979) observed that water stress decreased vegetative growth, tillers, root dry weight and axes number. Leach (1980) reported that the main effect of water stress during the growing season was decreasing number of tillers and premature senescence of leaves, which resulted in 40% reduction in leaf area. Musick and Grimes (1961) reported that sorghum is very sensitive to stress just before booting. Shipley and Regier (1970) indicated that plant sensitivity to stress increased in the period between heading and blooming more than mid-to-late booting. In addition, Lewis et al. (1974) concluded that the stress-sensitive period is during boot to bloom.

Moisture stress has a large impact on yield. Therefore, the relationship between grain yield of a sorghum crop and net amount of water applied throughout the season to soil moisture percent which was renewed weekly, regardless of

genotypes or plant stages under water stress, was found to be linear (Garrity et al., 1982a).

#### Moisture Stress Indication and Plant Adaptation

Drought resistance means that moisture stress effect on growth inhibition is relatively less or not severe (Blum and Sullivan, 1986). Drought resistance is divided into two parts: drought tolerance and drought avoidance. Drought tolerance is the extent to which plant functions are more or less successfully continued even throughout internal water stress. Drought avoidance is the extent to which the plant water status is continued under the presence of environmental drought (Hall et al., 1979). Hsiao et al. (1976) mentioned that, depending on drought exposure history, plants may respond differently to deficits of moisture. In the last few years several research tests have been conducted on drought resistant physiology (Paleg and Aspinall, 1981; Blum, 1982; Christiansen and Lewis, 1982). As of now, there is little information available about the relationship and effect of individual drought resistant physiological attributes (Blum and Sullivan, 1986). Wenzel and Van den Berg (1987) noted that despite our knowledge that the major factor limiting production is moisture stress, little has been accomplished in producing water-stress resistant varieties, because it is difficult to accurately determine drought resistance and hard

to produce uniform water stress in the open area of the test field. So crop improvement programs to produce drought resistant genotypes should work with large numbers of lines to get real genotypic differences. Clarke and McCaig (1982a) suggested that methods of assessing moisture stress must be rapid enough to select relatively large numbers of lines and accurate enough to detect real genotypic differences to be useful in selection programs for breeding for improved drought resistance. To differentiate genotype responses to water stress, different physiological indications have been used (Clarke and McCaig, 1982b; Singh et al., 1983). Clarke and McCaig (1982b) also stated that numerous techniques have been used for detecting water stress intensity in crops.

Stomatal activity has been used as an indicator of water stress (Ackerson, 1983; Garrity et al., 1984). Sorghum genotypes showed high stomatal conductance in well-watered plots and low stomatal conductance in high soil moisture stress plots (Wenzel and Van den Berg, 1987). Ceccarelli (1984) observed that crops can be screened for their degree of drought tolerance by using differential stomatal resistance to moisture stress. Bansal and Nagarajan (1986) concluded that stomatal conductance was the preferred indicator for drought resistance over leaf moisture content and proline accumulation.

Leaf temperature and temperature differential have been mentioned as helpful indicators of plant moisture stress (Clarke and McCaig, 1982a, 1982b; Singh and Kanemasu, 1983). Plant moisture status can be indicated by either leaf or canopy temperature because plant temperatures are associated with moisture stress (Sumayao et al., 1980; Idso et al., 1981). Jackson et al. (1977) stated that canopy temperature minus air temperature may be used as a valuable indicator of detecting the plant moisture content level.

Photosynthesis has been widely used as a measurement for drought tolerance (Jones and Rawson, 1979; Clarke and McCaig, 1982b; Ackerson, 1983; Garrity et al., 1984). Turner (1986) reported that leaf photosynthesis and leaf conductance were correlated with the soil moisture status. Fukushima et al. (1985) observed that leaf moisture status has a direct impact on photosynthesis activity.

Moisture stress effect on plant growth can be indicated by the decreasing number of green leaves, shorter plants, fewer heads, increasing specific leaf weight, and increasing leaf-stem dry weight ratios as observed in wheat plants by Hang and Miller (1983).

Plants adapt themselves to moisture stress in different ways. Wenzel and Van den Berg (1987) concluded from their research that sorghum genotypes adapted to drought in different ways, such as adjusting transpiration rate to soil

moisture availability. Pandey et al. (1984a, 1984b) observed that grain legumes partially avoid drought by reducing transpiration which results from low leaf area. Turner (1986) reported that the powerful tool for reducing water loss is stomatal closure. He also mentioned that around midday, leaf rolling is sharing in reducing water loss. Thus, the reduction in water loss postpones dehydration of leaf tissue and slows the soil moisture deficits. Turk and Hall (1980) stated that increased leaf senescence resulted in less water use as a result of leaf area reduction which could be observed as a way of drought avoidance. Termaat et al. (1985) stated that leaf area reduction is related to soil moisture status and root hydration. Small leaf area in small size plants was not the only plant factor working on maintaining leaf water potential. The high root length-density to leaf area ratio was also effective (Blum and Arkin, 1984). Root dry weight was considered by Shioh-Long (1981) as a good selection criteria identifying tolerant genotypes. He added that the roots of the tolerant genotypes travel to a deeper depth under dry conditions. Extraction of soil moisture under drought was determined by location and density of plant roots (Jordan and Miller, 1980; Turner, 1986). The sorghum plant tolerates moisture stress by maintaining a large root/shoot ratio and durability of green leaf area through grain filling period (Wright et al., 1983). Total plant

growth reduction, as a result of drought effect, ordinarily does not have that much inhibiting effect on root growth (Malik et al., 1979).

Osmotic adjustment, proline accumulation, and hormone level are used by plants for moisture stress adaptation. In stressed plants, osmotic adjustment may be the important component of crop performance stability (Morgan, 1984; Blum and Sullivan, 1986). Matsuda and Riazi (1981) stated that in barley plants, an important adaptive response to water stress is osmotic adjustment, which is lately being accepted as a fact. In sorghum leaves exposed to moisture stress create adaptation within themselves to the stress condition by reducing their osmotic potential (Fererres et al., 1978; Ackerson et al., 1980). Blum and Sullivan (1986) observed that sorghum and millet genotypes of considerable small size or small leaf area showed more osmotic adjustment and a high carbon exchange rate (CER) per unit leaf area under moisture stress. They added that the greater osmotic adjustment may be related to an increase in solute concentration which may be created by high CER in these plants. Zimmerman (1978) stated that as cell size got smaller, the osmotic adjustment got larger. Free proline accumulated in leaves as a result of moisture stress effect, but in resistant genotypes its content was low (Levy, 1983). From this, he suggested that leaf proline content and relative stress tolerance were

negatively correlated. Hanson et al. (1979) found that high water stress resulted in high significant proline accumulation in barley plants. Endogenous plant hormones may contribute in water stress plant adaptation. For example, Wiersma and Christie (1987) observed that in the guard cells, proline and abscisic acid increased by as much as seven-fold when plants are subjected to water stress. Jones and Mansfield (1970) speculated that abscisic acid was involved in regulating stomatal aperture in water stressed plants. Kannangara et al. (1982) proposed that in evaluating drought resistance, some of the endogenous plant hormone levels might prove helpful.

In general, the results of measuring physiological plant functions such as carbon exchange rate-transpiration ratio (CER/transpiration), leaf diffusive resistance, leaf water potential, and osmotic adjustment indicated that sorghum resists drought better than millet (Blum and Sullivan, 1986). Rosenow and Clark (1980) observed that sorghum genotypes could not resist moisture stress at both pre- and post-flowering stages, but they could tolerate it at either stage. Finally, Wenzel and Van den Berg (1987) concluded that initial leaf moisture content, excised leaf water retention capacity (ELWRC, defined as "the loss of water within the 3-hr periods expressed as a percentage of the total dry matter of each leaf") and head development were

the only characteristics appropriate to distinguish sorghum genotypes from each other. Thus it could be assumed that selecting among genotypes for water deficit resistance could not be related to transpiration, canopy temperature or diffusive resistance.

### Single Line Irrigation System

A single line irrigation system is used to provide a wide range of soil moisture, thereby facilitating measurements of physiological and agronomic characteristics of any crop under a continuous range of water levels (Hanks et al., 1976, 1980). The single line system was a practical technique enabling selection of genotypes according to their moisture stress resistance ability (Sullivan et al., 1980; O'Neill et al., 1983). The sprinkler gradient was successfully applied with sorghum (Sorghum bicolor L. Moench) (Chaudhuri and Kanemasu, 1982; O'Neill et al., 1983; and Garrity et al., 1984), pearl millet (Pennisetum americanum (L.) Leek) (Ibrahim et al., 1985; Osman, 1988), corn (Zea mays L.) (Sullivan et al., 1980), wheat (Triticum aestivum L. em. Thell.) (Hang and Miller, 1983), sugar beet (Beta vulgaris L.) (Miller and Hang, 1980), dry beans (Phaseolus vulgaris L.) (Pandey et al., 1984a, 1984b), and cow peas (Vigna unguiculate L. Walp ssp.) (Pandey et al., 1984a, 1984b).

The line source irrigation system provides nearly uniform water distribution parallel to the source line and perpendicularly to the same irrigation line, resulting in a continuously decreasing amount of water away from the irrigation line source (Sullivan et al., 1980). The sprinkler gradient system has many advantages such as: (1) economical and simple to operate and to install, (2) minimizing the land needed, and (3) providing continuous water from excess to nearly no water (Hanks et al., 1976). The sprinkler pattern can be altered by low-speed winds (Hanks et al., 1976); but this altering can sometimes be minimized by irrigating in the early morning or in a calm period and installing the line parallel to the common wind direction through the season. The irrigation amount is systematically applied without full randomization, creating a statistical problem of testing of the irrigation level effects (Hanks et al., 1980; Nelson and Rawlings, 1983). If the treatments are less than continuous and randomized within the gradient, statistical testing can then provide errors for analyzing the variables' effects and their interaction with the water levels. Hanks et al. (1980) mentioned that the statistical analysis for irrigation levels effect is not crucial because the effects of irrigation are always large. To avoid statistical cloudiness that may result from non-randomization of the water levels, applying selecting the best treatment test may give a reasonable

answer because it deals with treatments under each water level separately regardless of randomization of water levels. Lentner and Bishop (1986) reported that agronomists frequently use this test to select the best cultivar and its substitutes among some new cultivars grown under a certain condition.

## MATERIALS AND METHODS

This field experiment was conducted during the summer of 1984 at the Campus Agricultural Center (CAC), Tucson, Arizona. The purpose of the experiment was to study and compare the photosynthesis characteristics and plant growth and development of plants with seven different sorghum cytoplasms represented by nine lines under variable soil moisture stress (Table 1).

Lines one through seven had different cytoplasms from different taxonomic sources (Ross and Hackerott, 1972). These seven different cytoplasms had been previously classified as possessing an  $A_1$  cytoplasm sterility system type as found in milo cytoplasm and identified by Stephens and Holland in 1954 (Quinby, 1980). Lines eight and nine had been classified as having the  $A_2$  cytoplasm sterility system which was released by Schertz in 1976 (Schertz, 1988; Schertz et al., 1981). The  $A_2$  basic cytoplasms are considered to be from the same sorghum bicolor species as ACK-60 (line 1, Table 1). " $A_2$ " cytoplasm is different from " $A_1$ " cytoplasm in sterility response (Schertz, 1977). From a genic standpoint, the first seven lines contain identical genomes, which they inherited from their male parent (CK60); but the other two lines had different genomes, which came from their

Table 1. Seven sorghum cytoplasms represented by nine lines, evaluated for photosynthesis and related physiological characteristics under an irrigation gradient system.

Entry No.	Line	Species	Identification
1	ACK-60	<u>Sorghum bicolor</u> (L.) Moench	Day milo, C1959
2	AKS-34	<u>S. arundinaceum</u> Staph.	SA1741
3	AKS-35	<u>S. arundinaceum</u> Staph.	PI258806
4	AKS-36	<u>S. verticilliflorum</u> Staph.	PI208190
5	AKS-37	<u>S. sudanense</u> (Piper) Staph.	PI247722
6	AKS-38	<u>S. conspicuum</u> Snowden	PI155140
7	AKS-39	<u>S. niloticum</u> (Staph. ex piper)	Kenya 53262
8	A <sub>2</sub> TX398	<u>S. bicolor</u> (L.) Moench	IS12662CxBTx398
9	A <sub>2</sub> TX2788	<u>S. bicolor</u> (L.) Moench	A <sub>2</sub> TAM428xR1750

respective male parents. The male parent of line (8) was (BTX398) (Schertz, 1988) and the male parent of line (9) was (R1750) (Schertz et al., 1981).

The nine lines were evaluated for photosynthetic reaction under a soil moisture gradient. The soil moisture gradient was produced under a single line sprinkler system that applies water to the soil in decreasing amounts out from the line of sprinklers (Hanks et al., 1976).

The HSU's procedure for selecting the best treatment was used for statistical analysis (Kuehl, 1988). Agronomists are using this procedure for determining the best treatment and its substitutes under certain conditions (Lentner and Bishop, 1986). It does not test hypothesis but it determines which treatment is the best and which is or are its substitutes.

The three water levels could not be randomized because of using a single line sprinkler irrigation source and because of limited available experimental land area. Thus, the experiment was run with only two replications, making it necessary for the statistical analysis to be done separately for each water level in a randomized complete block design. The error mean squares (EMS) obtained were used for calculating the standard error of the means of the three observation times for the nine cytoplasm lines under each water level.

A fertilizer containing nitrogen and phosphorus (16-22-0) was broadcast preplant on the field at the rate of 250 kg/ha. The field was then disked and furrowed out for planting. Seeds of each of the nine genotypes were planted on 26 April 1984 at a rate of 18 seeds/m in moist soil on beds spaced 1 m apart, running parallel to the sprinkler line. The plots were 3 m long (plot size 1 m x 3 m), with 30 cm alleys. The seed beds were pre-irrigated by furrow irrigation once then irrigated again to field capacity immediately after planting. Three furrow post-plant irrigations, two of which were alternate furrow irrigations and one was full irrigation totaling approximately 300 mm of water, were applied to the three soil moisture level treatments before the sprinkler irrigation system was put into place.

The emerged plant stands were hand thinned to a uniform spacing of about 10 cm between plants. Sudangrass hybrid seeds were hand planted in the gaps of missing sorghum plants to create a more uniform stand competition pattern to reduce the likelihood of unequal competition among plants. Sudangrass plants were kept cut to the height of adjacent sorghum plants to avoid the effect of shading on adjacent sorghum plants. Broadleaf weed control was obtained by applying atrazine (2-chloro-4-ethylamino-6-isophrophylamino-S-triazine) at a rate of 1.75 kg/ha of active ingredi-

ent at the three-leaf stage of seedling growth. Narrow leaf weeds were removed by hand.

The irrigation gradient sprinkler system was then installed at the five-leaf stage (Maiti and Bidinger, 1981), to supply all future moisture to the plots. The system consisted of a single line of sprinklers located at the center of the experimental field, parallel to the crop rows. The sprinkler line applied a continuous moisture gradient in decreasing amounts out from the center of the field on both sides of the sprinkler line. The experiment was sprinkler-irrigated initially about twice a week in the early mornings when wind speeds were low and continued for about 1 hour, with a uniform sprinkler line pressure of 30 psi. Later in the growing season, when plants were larger and used water at an increasingly faster daily rate, sprinkler irrigations were applied three times a week. The amount of water applied was measured by catch-cans, at the high, medium, and low gradient water application points. The top of the catch-can holder cylinders were cut at a slope. The top openings of catch-cans themselves were level. The catch-can holder heights were decreased in height gradually from the high water level to the low water level (140, 125, 110 cm) to catch the proper amount of the water drops emitted by the sprinklers and from rainfall. The amount of water received

by low and medium water levels were compared with the amount received by the high water level.

Soil access tubes to a 1 meter depth were placed at locations at a distance of 1.5, 7.5, and 12.5 meters from the line source under the gradient at the points where high, medium, and low water applications were received.

Soil samples were taken from 30, 60, and 90 cm depths at neutron probe access tube sites for measuring soil moisture tension and for comparing them with neutron probe data for calibration purposes. The depths of the soil samples were the same as used by Nakayama and Reginato (1982) for moisture contents gravimetric determination and for neutron probe calibration in the field. A Campbell Pacific neutron moisture meter, Model 503, was used to estimate soil water content at the three plant physiological data collecting times during the period between 1 June and 13 July 1984. Sprinkler irrigations were applied two times a week early in the 1 June to 13 July time interval and three times a week during the latter part of this time period. Four irrigations were selected at weekly intervals during the 1 June to 13 July time period for plant physiological and neutron probe data collection. These irrigations occurred at 58, 65, 72 and 79 days after planting. Plant physiological data were collected immediately following the irrigation on the 58th, 72nd, and 79th day. Plant physiological data were collected

on day 64 just prior to the irrigation on day 65. Neutron probe data were collected the day before or about 17 hours prior to the irrigations and again about 7 hours after completion of the irrigations on the 58th, 65th, and 72nd day. Plant physiological readings were taken on the 79th day but no neutron probe data were collected because of heavy rain on all soil moisture treatments. The fourth plant physiological data collection from the 79th day was discarded because rainfall removed the effect of water stress.

Sorghum genotype physiological evaluations were made at these field locations as representative of low, medium, and high soil moisture stress on the plants. Photosynthesis of the nine cytoplasm lines under the three soil moisture stress levels were evaluated by collecting data from one typical plant per plot from each water level (two plants per treatment). The measurements were started 3 weeks after the water stress was imposed. Measurements were taken for:  $\text{CO}_2$  exchange, specific leaf weight, leaf transpiration, leaf diffusive resistance, leaf temperature, and temperature differential.

Apparent photosynthesis was determined four times at weekly intervals using the methods of Clegg and Sullivan (1976) and Sullivan et al. (1976). The fourth and last set of data was not included in the statistical analysis because of the effect of an immediately prior rainfall, which

alleviated the effect of water stress. The sorghum plants previously under stress recovered to a non-stressed condition (Appendix A). Patterson et al. (1979) recognized that fast recovery of leaf water potential that occurred in stressed soybean plants consequent to rewatering, but net CO<sub>2</sub> exchange rate took several days after leaf water potential recovery to return to the normal situation of well irrigated plants of the same growth stage. Jones and Rawson (1979) concluded that rewatering of stressed sorghum plants brings water potential to control levels within 12 hours, but photosynthesis and leaf conductance are recovered from the stressed condition by 3 days from the rewatering. Patterson (1986) also pointed out that water stress increased specific leaf weight in C<sub>4</sub> grasses and rewatering decreased it, but in soybean SLW also tended to increase throughout drought and recovery times.

For rate of photosynthesis measurements, a measured leaf area was enclosed in a plexiglass chamber with circulating air for 30 seconds. Air samples were taken with syringes at the beginning and end of this 30-second time period. A Beckman model 865 infrared gas analyzer described by Clegg et al. (1978) was used to measure the CO<sub>2</sub> present before and after the 30 seconds. The differential was a measure of rate of photosynthesis.

The leaf area of full mature upper selected leaves per plant per plot was determined by using a LI-Cor Model 3100 leaf area meter.

The photosynthetic rate was calculated by the equation of (Muramoto et al., 1967):

$$\text{Net PS in mg CO}_2\text{dm}^{-2}\text{hr}^{-1} = \frac{44,000\text{mg CO}_2/\text{mole} \times 10^{-6} \times \text{chamber volume} \times \frac{\text{dppm}}{\text{liter}} \times \frac{273}{\text{T}} \times \frac{760}{\text{atm}} \times 3600}{\text{dm}^2 \text{ (leaf area)}}$$

where

ps = photosynthesis,

44,000 = CO<sub>2</sub> molecular weight in mg,

22.4 L = volume of one mole of gas in liters,

10<sup>6</sup> = umoles in one mole,

chamber volume = 2.364L,

dppm =  $\frac{\text{difference in CO}_2 \text{ concentration between two syringes}}{30 \text{ seconds}}$

T = ambient temperature + K,

Atm = atmospheric pressure (mm Hg),

3600 = conversion from seconds to hours.

Hence, the net photosynthesis in umoles CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> is calculated by multiplying net photosynthesis in mg CO<sub>2</sub> dm<sup>-2</sup> hr<sup>-1</sup> times 0.6313

where

$$0.6313 = \frac{\text{mg CO}_2}{\text{dm}^2} \times \frac{1}{\text{hr}} \times \frac{100 \text{ dm}^2}{\text{m}^2} \times \frac{\text{hr}}{3600} \times \frac{10^6 \text{ umole}}{44,000 \text{ mg}}$$

where

0.6313 = constant coefficient

hr = hour,

100 =  $\text{dm}^2/\text{m}^2$  (Osman, 1988).

Transpiration ( $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ ), diffusive resistance ( $\text{s cm}^{-1}$ ) and leaf and ambient temperature ( $^{\circ}\text{C}$ ) were measured with a Licor model LI-1600 steady state porometer.

## RESULTS AND DISCUSSION

### Irrigation Water

A single line sprinkler irrigation system supplied water in decreasing amounts with increasing distances from the irrigation line. The correlation coefficient of the relationship between the gradient of amounts of water applied and distances from the irrigation line was  $r = 0.98$  (Figure 1a). The mean amounts of water applied at low, medium and high water levels were 34.68, 44.05 and 49.72 cm, respectively. Actual amounts of water received by each sorghum entry under each water level are graphically presented in Figure 1b. These water amounts were close to the grand mean for all entries for each water level, with standard errors of 0.367, 0.310 and 0.947 of low, medium and high water levels, respectively (Table 2). Hence, all nine entries received quite uniform applications of irrigation water at each water level for the entire 10 week growing season from date of planting. Therefore, different results will be related to differences between water levels.

### Soil Moisture

The soil texture at a depth of 30 cm was 53.6% sand, 29% silt and 17.3% clay; at a 60 cm depth it was 81.3% sand, 11.8% silt and 6.9% clay (Ibrahim, 1984). At 90 cm depth the

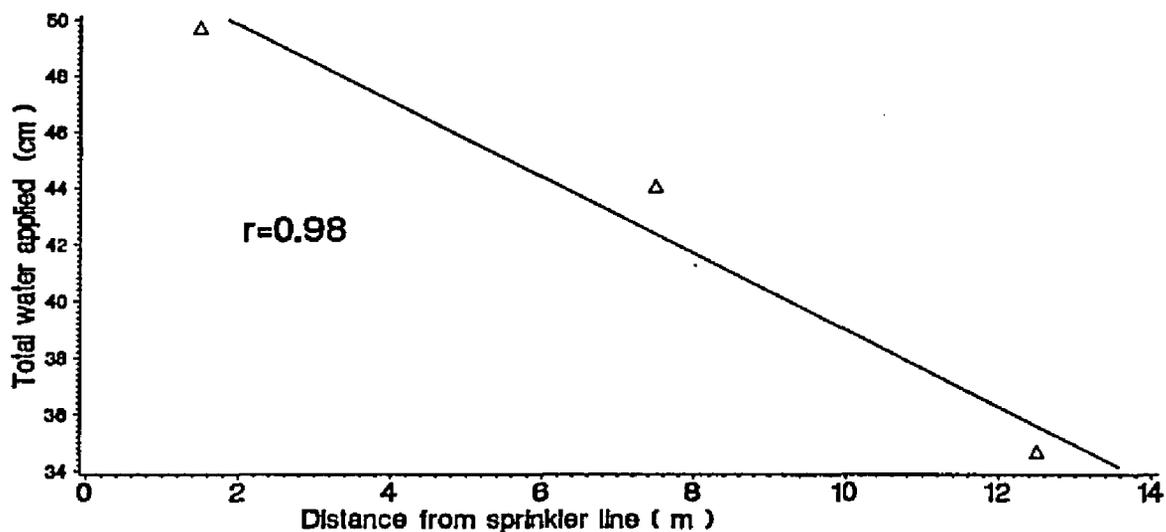


Fig.1a. Regression line of total water amount means applied and distance from the irrigation sprinkler line ( m ).

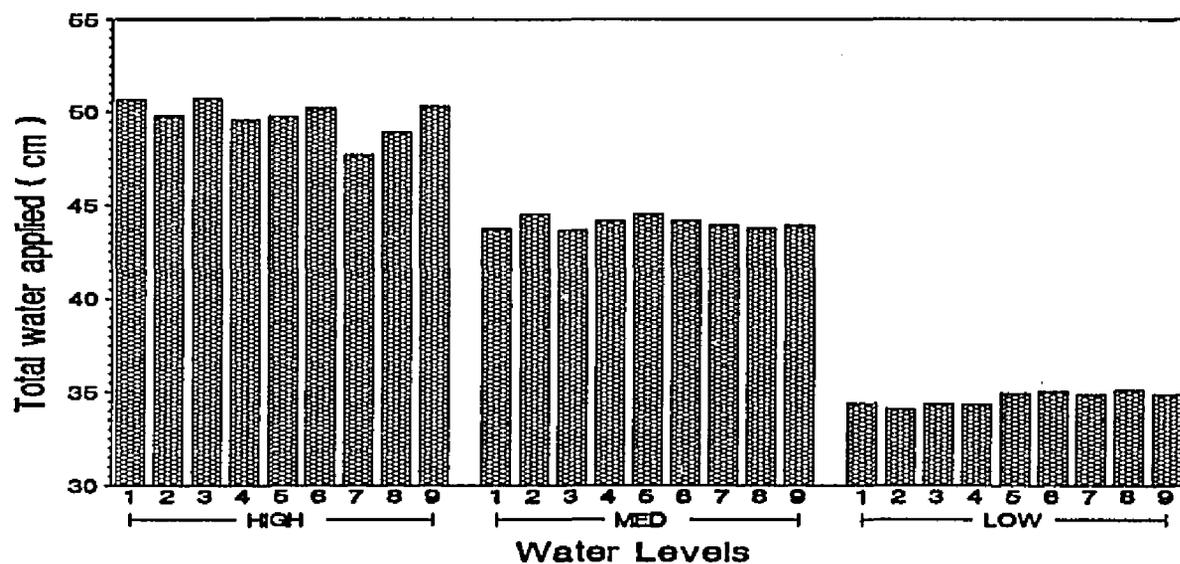


Fig.1b. Total water applied during 10 weeks after planting to nine sorghum lines under high, medium and low water application levels.<sup>1</sup>

- |          |          |          |            |             |
|----------|----------|----------|------------|-------------|
| 1) ACK60 | 3) AKS35 | 5) AKS37 | 7) AKS39   | 9) A2TX2788 |
| 2) AKS34 | 4) AKS38 | 6) AKS38 | 8) A2TX398 |             |

Table 2. Means of total water amounts applied to nine sorghum lines under the three water levels during the beginning 10 weeks of the growing season.

	Lines	Water Amounts Applied (cm)		
		Water Levels		
		Low	Medium	High
1	ACK60	34.38	43.75	50.68
2	AKS34	34.12	44.51	49.77
3	AKS35	34.39	43.68	50.70
4	AKS36	34.35	44.19	49.57
5	AKS37	34.96	44.49	49.72
6	AKS38	35.04	44.20	50.17
7	AKS39	34.87	43.93	47.71
8	A <sub>2</sub> Tx398	35.12	43.79	48.88
9	A <sub>2</sub> Tx2788	34.89	43.93	50.29
Grand mean		34.68	44.05	49.72
Standard error		0.367	0.310	0.947

soil texture was coarse sand, gravel and almost no clay, causing it to have a very low water holding capacity.

The soil moisture percent (by volume) was calculated using the calibration curve of the neutron probe (Figure 2). The correlation coefficient ( $r$ ) was 0.86. Figure 3 showed that soil moisture was uniformly consistent at the high water level to low water level at 30 and 60 cm soil depths. At the 90 cm soil depth, soil moisture was high at the high water level and lowest under the medium water level. A variation in soil moisture content over the 24 hour intervals, before and after the irrigation on days 58, 65 and 72 at the 30 cm soil depth was very pronounced under high and medium water levels. Under the low water level (high water stress), there was very little change in soil moisture percent from the irrigations. The percentage of water available in the soil at low water level was much less than at the high water level. At the three soil depths, the soil moisture content decreased gradually throughout the entire growing season. This decrease was more uniform at the 60 cm soil depth than at the other two soil depths. This less variable decrease in soil moisture content over time at the 60 cm soil depth suggests that the irrigations replenished very little of the moisture that has been extracted by the roots at the 60 cm soil depth. Replenishment of soil moisture at the 90 cm depth during the growing season was even less than at the 60 cm depth.

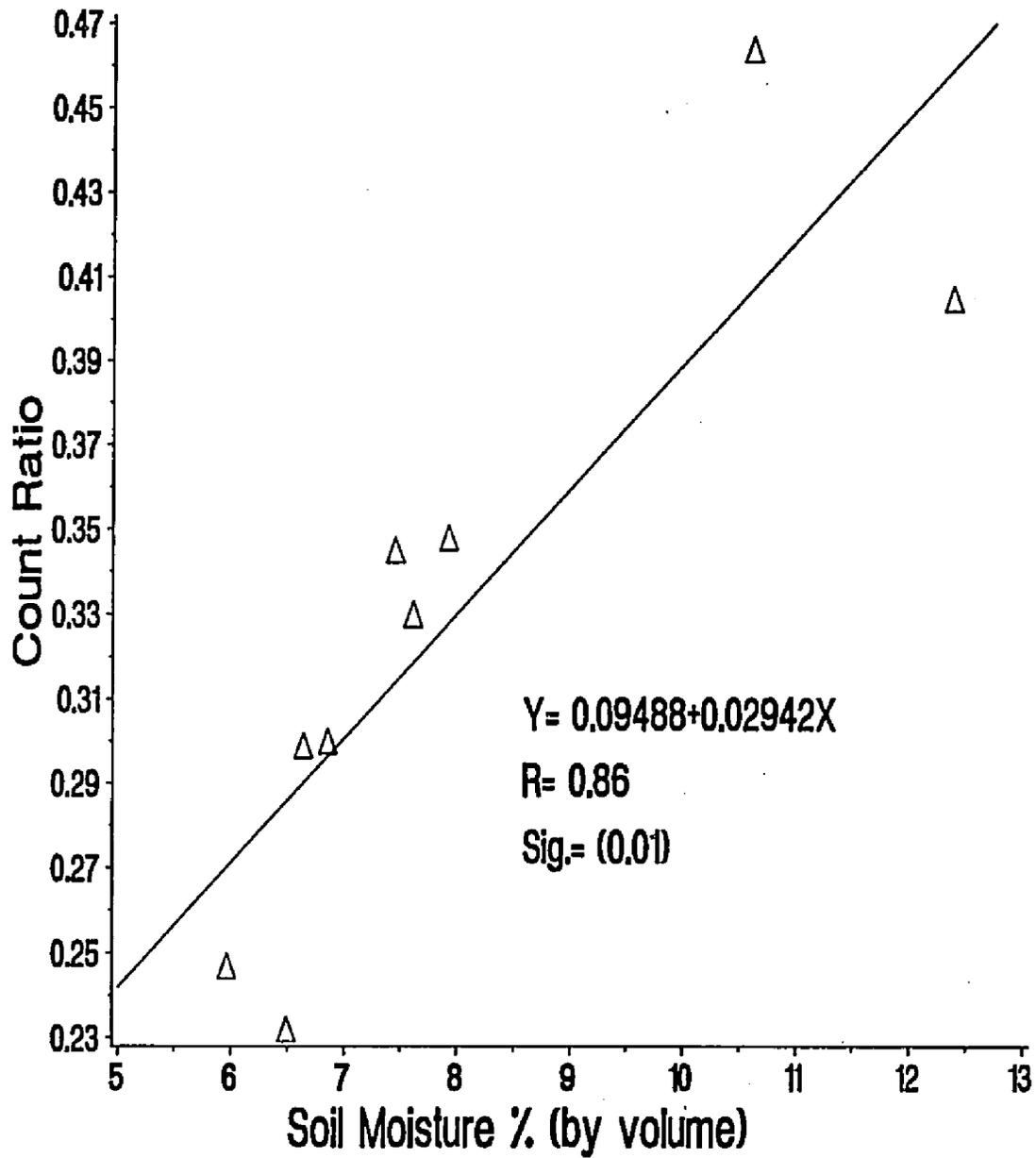


Fig.2. Neutron probe calibration curve at three soil depths of 30, 60 and 90 cm at the CAC.

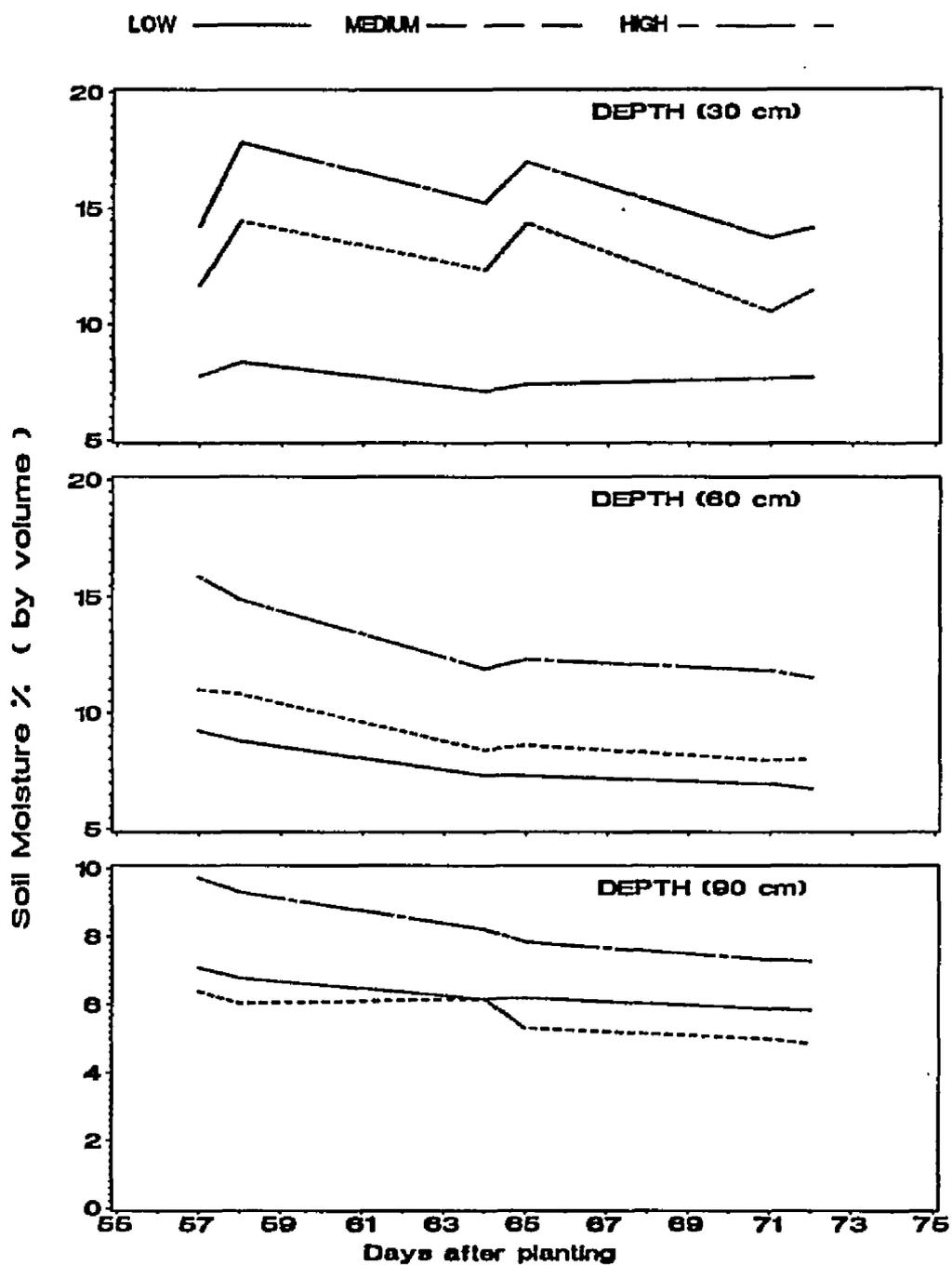


Fig.3. Soil moisture % (by volume) at 30, 60, and 90 cm depths and three irrigation levels low, medium and high.

At the 90 cm soil depth the water holding capacity of the gravelly soil texture was very low. Thus, the plant root systems could extract only a small amount of soil moisture before the soil moisture content reached a low level, at which the plant roots could no longer absorb water.

### Physiological Aspects

The mean responses of the nine sorghum lines for six plant physiological functions under high, medium and soil moisture non-stress levels are presented in Figures 4, 5 and 6. These physiological responses were measured at the 8, 9, and 10 week periods of growth and development. The 10 week period started from the planting date up to floral development.

Apparent photosynthesis and transpiration rates (Figure 4) all decreased with decreasing amounts of available soil moisture. Diffusive resistance (Figure 5) and leaf temperature (Figure 6) all increased with decreasing amounts of available soil moisture. Temperature differential (Figure 5) and specific leaf weight among lines varied in response to changes in available soil moisture (Figure 6).

### Apparent Photosynthesis

The apparent photosynthesis mean response rates of the individual nine lines to high and medium soil moisture stress, as illustrated in Figure 4, were compared to the soil moisture

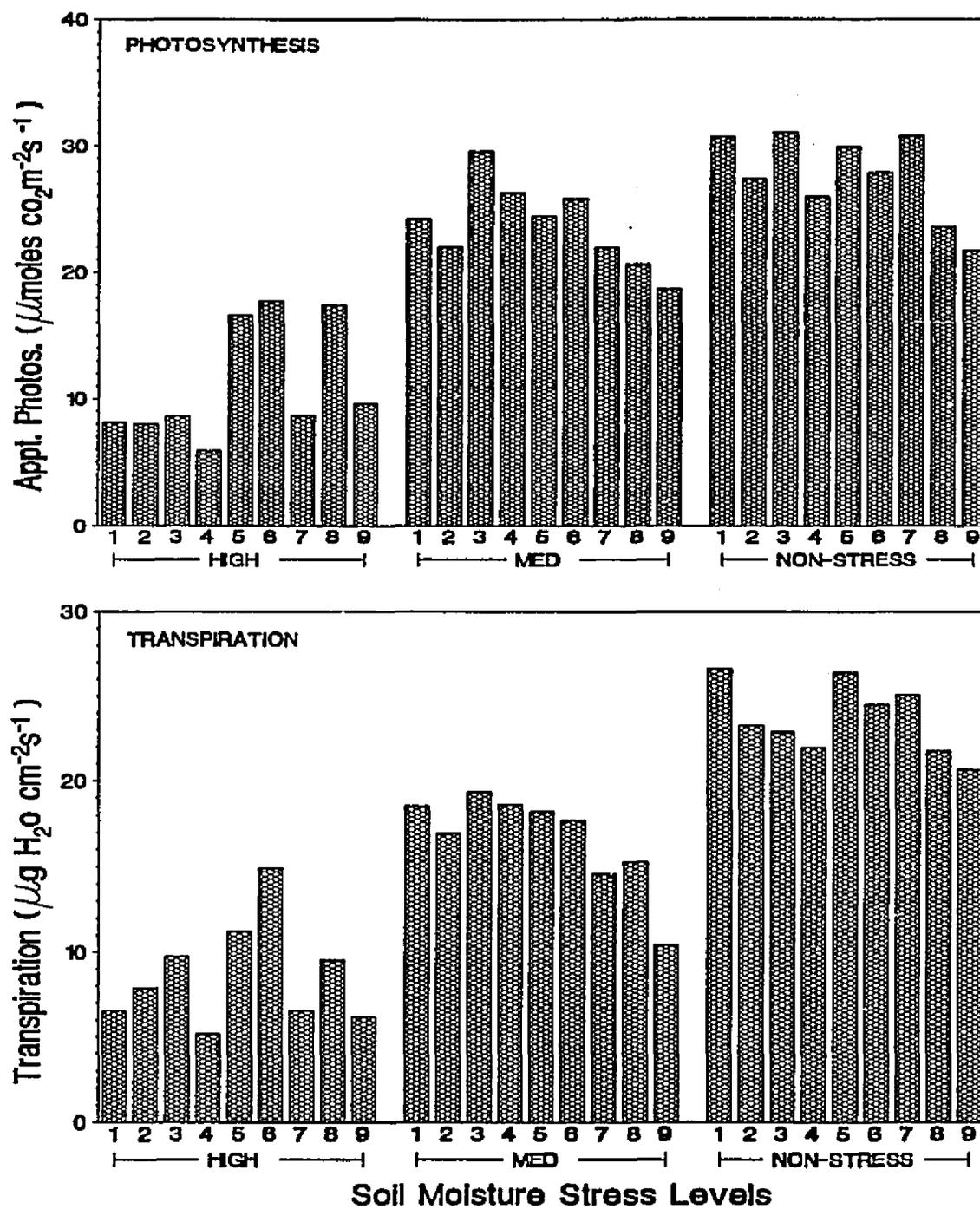


Fig.4. Mean responses of leaf apparent photosynthesis and transpiration over 10 weeks after planting of nine sorghum lines grown under high, medium and non-stress soil moisture stress levels.<sup>1</sup>

1/ 1) AKS60    3) AKS35    5) AKS37    7) AKS39    9) A2TX2788  
 2) AKS34    4) AKS36    6) AKS38    8) A2TX388

non-stress level (high water level). High soil moisture stress caused large and variable declines in photosynthesis rates among the nine lines. These reductions ranged from 26% for A<sub>2</sub>TX398 to 77% for AKS36. The medium soil moisture stress also caused decreases in photosynthesis rates for all nine lines. These declines were more moderate in magnitude and also varied among the lines ranging from 0% for AKS36 to 29% for AKS39.

The photosynthesis rates under soil moisture non-stress (high water level) were all high, ranging from 21.73  $\mu\text{moles CO}_2\text{m}^{-2}\text{s}^{-1}$  for A<sub>2</sub>TX2788 up to 31.05 for AKS35 (Table 3). The highest reduction in photosynthesis rate of 77% for AKS36 from high soil moisture stress was also obtained in pearl millet by Osman (1988). The low decrease in rate of photosynthesis of 26% is similar to that observed in sorghum by Garrity et al. (1984), who had reductions ranging from 14 to 26% under what he called high soil moisture stress.

The line AKS38 showed the highest photosynthesis rate of 17.75  $\mu\text{moles CO}_2\text{m}^{-2}\text{s}^{-1}$  under the low water level (high soil moisture stress); therefore, it was used as the standard for comparison among all lines for photosynthesis rates (Table 3).

Lines A<sub>2</sub>TX398 and AKS37 had rates of photosynthesis of 17.41 and 16.61  $\mu\text{moles CO}_2\text{m}^{-2}\text{s}^{-1}$ , respectively, which were significantly similar to AKS38 and different from the other six lines at a 5% confidence level. AKS38, A<sub>2</sub>TX398 and AKS37

Table 3. Means of apparent photosynthesis for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

		Apparent Photosynthesis ( $\mu\text{moles CO}_2\text{m}^{-2}\text{s}^{-1}$ )		
		Soil Moisture Stress Levels		
Lines		High	Medium	Non-stress
1	ACK60	8.15 N	24.19 Y	30.67 Y
2	AKS34	8.04 N	22.05 Y	27.38 Y
3	AKS35	8.63 N	29.57 Y	31.05 Y
4	AKS36	5.90 N	26.24 Y	25.97 Y
5	AKS37	16.61 Y <sup>(1)</sup>	24.44 Y	29.93 Y
6	AKS38	17.75 Y	25.82 Y	27.83 Y
7	AKS39	8.70 N	21.97 Y	30.79 Y
8	A <sub>2</sub> TX398	17.41 Y	20.68 Y	23.58 N
9	A <sub>2</sub> TX2788	9.60 N	18.71 Y	21.73 N

<sup>1/</sup> Values followed by (Y) letter in the same column are the best ones at 0.50 significant level (i.e., the probability of correct selection  $[P(\text{CS}) = (1 - \alpha)]$  is 95% according to Hsu's procedure for selecting the best treatment in a subset.

may all be considered as equal in rate of photosynthesis under high soil moisture stress and substitute for each other.

The photosynthesis rates of all nine lines under the medium soil moisture stress level were significantly high at the 5% level and were not statistically different from each other. The highest photosynthesis rate at the medium soil moisture stress level was  $29.57 \text{ umoles CO}_2\text{m}^{-2}\text{s}^{-1}$  by AKS35 (Table 3). Statistically, all the other eight lines are considered as substitutes for line AKS35. Because all nine lines behaved similarly for rate of photosynthesis under medium soil moisture stress indicates that all seven cytoplasms represented by the nine lines could tolerate the medium soil moisture stress of this test without statistically significant reductions in photosynthesis rates.

The highest rate of photosynthesis at the high water level (soil moisture non-stress) was obtained by line AKS35, with a rate of  $31.05 \text{ umoles CO}_2\text{m}^{-2}\text{s}^{-1}$ , making AKS35 as the statistical standard for the soil moisture non-stress level (Table 3). The lines ACK60 and AKS34 to AKS39 were statistically similar to AKS35 at the 5% level. Lines A<sub>2</sub>TX398 and A<sub>2</sub>TX2788 were not significantly similar to AKS35 in their photosynthesis rates.

From the previous discussion, it can be concluded that the two extreme limits of soil moisture availability (high

stress and non-stress soil moisture stress levels) created the greatest differences among the nine different lines.

The significant differences in photosynthesis responses among the nine lines under the high soil moisture condition indicated that these differences in responses were related to the differences in cytoplasms as shown in Table 3. The first seven lines had different cytoplasms but the same genomes. So, the differences in their photosynthesis responses were due to their differences in cytoplasms.

The difference in responses between the last two lines (Table 3) may be related to the differences in their genomes because both had the same cytoplasms. Therefore, the differences in photosynthesis responses here seems to be due to nuclear control. Miles and Metz (1985) mentioned that the photosynthetic system is controlled by nuclear and chloroplast genes. The two genotypes, entries eight and nine, were statistically different under high water level (soil moisture non-stress) from the other seven and responded quite differently from each other under low water level (high soil moisture stress). A<sub>2</sub>TX398 had next to the lowest rate of photosynthesis under soil moisture non-stress but next to the highest rate of photosynthesis under high soil moisture stress. A<sub>2</sub>Tx398 seemed to be the least affected of all nine lines in rate of photosynthesis by changes in soil moisture stress. The early maturity line, A<sub>2</sub>TX398 (Table 4), had a

Table 4. Number of days from planting date to 50% heading of nine sorghum lines grown under high, medium and non-stress soil moisture stress levels.

Lines	ACK60	AKS34	AKS35	AKS36	AKS37	AKS38	AKS39	A <sub>2</sub> Tx398	A <sub>2</sub> Tx2788
Days between planting and heading	71	64	71	71	66	66	73	59	85

shorter vegetative growth period and began its reproductive growth phase earlier than the late maturity line A<sub>2</sub>TX2788. Therefore, the early maturity genotype used a smaller portion of its total water consumption for vegetative growth and had a greater portion left for reproduction of heads and grains. The late maturity genotype had a longer vegetative growth period, resulting in more leaves and leaf area. This resulted in greater transpiration and water use, which caused greater water use from the soil and higher soil moisture stress than the early maturity genotype. The higher soil moisture stress caused lower photosynthesis and transpiration rates and higher diffusive resistance relative to the early maturity genotype.

The first seven lines all possess exactly the same maturity genotypes. The differences in maturity may be due in part to some variation in soil moisture stress among the plots. The soil of the experimental site was quite variable, resulting in some variation in water holding capacity among plots.

Under the high water condition there was no soil moisture stress, so the photosynthesis response differences among the cytoplasms should be real differences in photosynthesis capabilities (Table 3). The A<sub>2</sub> sterility system cytoplasms were significantly different from the first seven lines, which were all A<sub>1</sub> sterility system cytoplasm.

All nine lines were not statistically different from each other for rate of photosynthesis under medium soil moisture stress. AKS37 and AKS38 were two of the significantly high group of three for rate of photosynthesis under high soil moisture stress but had only medium rates of photosynthesis under soil moisture non-stress. These variations in rates of photosynthesis among and within cytoplasm types suggest that there may be differences among photosynthesis systems which give variable performances under different levels of soil moisture stress.

#### Transpiration

The mean responses of the nine lines for transpiration under three levels of soil moisture stress, are presented in Figure 4. All transpiration rates decreased with increased soil moisture stress (decreasing soil moisture availability). Wenzel and Van den Berg (1987) reported that sorghum genotypes adjust transpiration rates according to availability of soil moisture. The percent reduction with increased soil moisture stress varied among lines. The highest percent reduction in transpiration rate due to high soil moisture stress compared to soil moisture non-stress was 76.5% for AKS36 and the lowest reduction was 39.1% for AKS38 (Table 5).

Under medium soil moisture stress the percent reduction in transpiration rates, as compared to soil moisture non-

Table 5. Means of transpiration rates for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

	Lines	Transpiration ( $\mu\text{g H}_2\text{O cm}^{-2}\text{s}^{-1}$ ) Soil Moisture Stress Levels		
		High	Medium	Non-stress
1	ACK 60	6.54 N	18.55 Y	26.60 Y
2	AKS 34	7.87 N	16.94 Y	23.24 Y
3	AKS 35	9.75 Y <sup>(1)</sup>	19.32 Y	22.87 Y
4	AKS 36	5.17 N	18.58 Y	21.96 Y
5	AKS 37	11.25 Y	18.20 Y	26.37 Y
6	AKS 38	14.93 Y	17.68 Y	24.50 Y
7	AKS 39	6.58 N	14.56 Y	25.09 Y
8	A <sub>2</sub> TX398	9.53 Y	15.25 Y	21.74 Y
9	A <sub>2</sub> TX2788	6.21 N	10.42 Y	20.66 Y

<sup>1</sup> Values followed by (Y) letter in the same column are the best ones at 0.05 significant level (i.e., the probability of correct selection  $[P(\text{CS}) = (1 - \alpha)]$  is 95% according to Hsu's procedure for selecting the best treatment in a subset.

stress, among all lines ranged from 15.4% for AKS36 to 46.6% for A<sub>2</sub>Tx2788 (Table 5).

The transpiration rates under high soil moisture stress at the low water level ranged from 5.17 ug cm<sup>-2</sup>s<sup>-1</sup> for AKSK36 to 14.93 ug cm<sup>-2</sup>s<sup>-1</sup> for AKS38. All lines, except AKS37 and AKS38, had transpiration rates lower than the rates obtained by Agbary (1985), which ranged from 11.50 to 16.20 ug cm<sup>-2</sup>s<sup>-1</sup> under different irrigation regimes on heavier soils. The transpiration rates under soil moisture non-stress ranged from 20.66 ug cm<sup>2</sup>sl for A<sub>2</sub>Tx2788 to 26.60 for ACK60 which are comparable to those obtained by Agbary (1985), which ranged from 20.30 to 28.50 ug cm<sup>-2</sup>s<sup>-1</sup>.

The transpiration rates of all nine lines were not statistically different under both the soil moisture non-stress and medium soil moisture stress levels. These statistically uniform ranges in transpiration rates were 20.66 to 26.60 ug cm<sup>-2</sup>s<sup>-1</sup> at the soil moisture non-stress level and 10.42 to 19.32 ug cm<sup>-2</sup>s<sup>-1</sup> at the medium soil moisture stress level (Table 5).

Under the low water level (high soil moisture stress), four lines, AKS38, AKS37, AKS35 and A<sub>2</sub>Tx398, in order of highest to lowest, had statistically greater transpiration rates as a group than the other five lines. Three of these four were also the statistically high three for photosynthesis under high soil moisture stress. AKS35 was not signifi-

cantly high for photosynthesis but was for transpiration. This may further indicate possible differences among cytoplasms for photosynthesis system differences under soil moisture stress.

Further comparison of the behavior among the nine lines for both photosynthesis and transpiration under high soil moisture stress showed that line A<sub>2</sub>Tx398 maintained a high photosynthesis rate with a low transpiration rate. This relationship may make it a good water stress tolerant genotype in terms of photosynthesis and transpiration rates. Line AKS38 maintained a high photosynthesis rate under high soil moisture stress, but its transpiration rate was also high. This relationship indicates that AKS38 would be less drought tolerant over a longer period of time by virtue of using more water under stress than A<sub>2</sub>Tx398.

Line A<sub>2</sub>Tx2788, under high soil moisture stress, had a 56% reduction in photosynthesis and a high 70% reduction in transpiration compared to under soil moisture non-stress. On the other hand, line AKS35, also under high soil moisture stress, had a high reduction in photosynthesis of 72% and a lower 57% reduction in transpiration compared to under soil moisture non-stress. These different magnitudes of reaction to soil moisture stress for photosynthesis and transpiration indicate a selection potential for improved drought tolerance among cytoplasms. Lines ACK60, AKS34 and AKS39 had high

reductions in both photosynthesis and transpiration under high soil moisture stress compared to soil moisture non-stress. Line AKS36 had the highest reduction in both photosynthesis and transpiration under high soil moisture stress compared to soil moisture non-stress. These four lines reacted to high soil moisture stress with very low transpiration rates, compared to soil moisture non-stress, which probably caused corresponding reductions in photosynthesis. These four lines must be considered quite susceptible to drought.

#### Diffusive Resistance

The mean responses of the nine sorghum lines for leaf diffusive resistance are presented in Figure 5. These results showed that diffusive resistance for all lines increased as soil moisture stress increased. These results are comparable to those reported by Wenzel and van den Berg (1987). They reported that sorghum varieties have low diffusive resistance under soil moisture non-stress and high diffusive resistance under high soil moisture stress. The amount of increase in diffusive resistance with increased soil moisture stress differed among lines. The increases in diffusive resistance, from high soil moisture stress, ranged from 2.34 times to 11.26 times the rate of low soil moisture stress for AKS38 and ACK60, respectively. The medium soil moisture stress level effect on diffusive resistance was for very modest increases

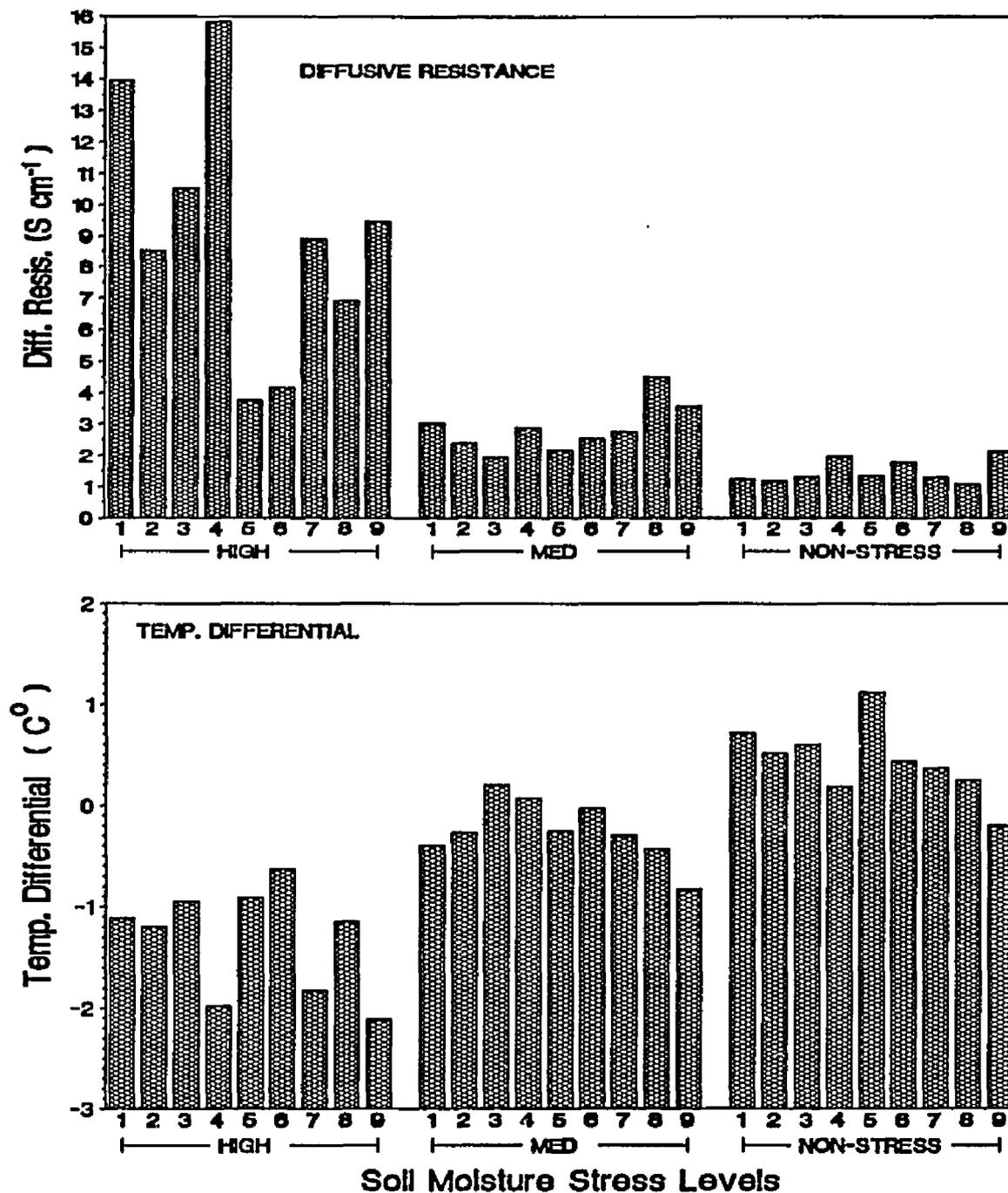


Fig.5. Mean responses of diffusive resistance and temperature differential over 10 weeks after planting of nine sorghum lines grown under high, medium and non-stress soil moisture stress levels.<sup>1</sup>

1) ACK60    3) AKS35    5) AKS37    7) AKS39    9) A2TX2788  
 2) AKS34    4) AKS38    8) AKS38    6) A2TX398

of 1.47 times the rate at low soil moisture stress for AKS35 and AKS36 to 4.17 times for A<sub>2</sub>Tx2788.

Diffusive resistance values under soil moisture non-stress ranged from 1.08 s cm<sup>-1</sup> for A<sub>2</sub>Tx398 to 2.12 for A<sub>2</sub>Tx2788 (Table 6). This range was similar to that reported by Agbary (1985) of 0.94 to 3.65 s cm<sup>-1</sup>. Under medium soil moisture stress, diffusive resistance ranged from 1.93 s cm<sup>-1</sup> for AKS35 to 4.50 for A<sub>2</sub>Tx398. Under high soil moisture stress the range of diffusive resistance among all nine lines was from 3.76 s cm<sup>-1</sup> for AKS37 up to 15.84 for AKS36. These high soil moisture stress diffusive resistance values were higher than those reported by Hofmann et al. (1984) of 1.16 to 4.81 s cm<sup>-1</sup> and Agbary (1985) of 2.81 to 13.3 s cm<sup>-1</sup>. The diffusive resistance range of this experiment was lower than that obtained by Blum (1974), who reported a high value for sorghum of 20.20 s cm<sup>-1</sup> under high soil moisture stress.

There was no statistically significant difference among the lines for diffusive resistance and transpiration under soil moisture non-stress and medium soil moisture stress (Tables 5 and 6). In other words, all nine lines showed high transpiration rates and low diffusive resistance values under these two soil moisture levels. Wenzel and Van den Berg (1987) observed that under soil moisture non-stress, transpiration and diffusive resistance were highly and negatively

Table 6. Means of diffusive resistance for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

	Lines	Diffusive Resistance ( $s\ cm^{-1}$ ) Soil Moisture Stress Levels		
		High	Medium	Non-stress
1	ACK 60	13.96 Y <sup>(1)</sup>	3.04 Y	1.24 Y
2	AKS 34	8.51 Y	2.38 Y	1.18 Y
3	AKS 35	10.53 Y	1.93 Y	1.31 Y
4	AKS 36	15.84 N	2.89 Y	1.96 Y
5	AKS 37	3.76 Y	2.16 Y	1.34 Y
6	AKS 38	4.16 Y	2.52 Y	1.78 Y
7	AKS 39	8.90 Y	2.75 Y	1.30 Y
8	A <sub>2</sub> TX398	6.92 Y	4.50 Y	1.08 Y
9	A <sub>2</sub> TX2788	9.47 Y	3.58 Y	2.12 Y

<sup>1</sup> Values followed by (Y) letter in the same column are the best ones at 0.05 significant level (i.e., the probability of correct selection [ $P(CS) = (1 - \alpha)$ ] is 95% according to Hsu's procedure for selecting the best treatment in a subset.

correlated, but under high soil moisture stress the correlation was low.

Under high soil moisture stress, line AKS36 was significantly higher for diffusive resistance than the other eight lines (Table 6). AKS36 had the highest level of diffusive resistance and the lowest rates of photosynthesis and transpiration, illustrating the negative relationship of diffusive resistance with photosynthesis and transpiration.

#### Leaf Temperature Differential

The leaf temperature differential is calculated by subtracting the leaf temperature from the ambient air temperature. These values for all nine lines at the three soil moisture stress levels are presented in Table 7. Under high soil moisture stress, the temperature differential values for all lines were negative, indicating that the leaves could not properly cool themselves at that soil moisture stress level. These results are in agreement with those of Pandey et al. (1984b). Leaf temperatures were increased by soil moisture stress.

Differences between ambient temperature and leaf temperature decreased in negative numerical values as soil moisture increased (decreased soil moisture stress) (Figure 5). These decreases in temperature differential with the increases in soil moisture were a result of a microclimate created in the high soil moisture level plots. The micro-

Table 7. Means of ambient temperature, leaf temperature and temperature differential for nine sorghum lines grown under high, medium and non-stress soil moisture stress levels.

		Soil moisture stress levels								
		High			Medium			Non-stress		
Lines		Leaf Temp. (C)	Ambient Temp. (C)	Diff. Temp. (C)	Leaf Temp. (C)	Ambient Temp. (C)	Diff. Temp. (C)	Leaf Temp. (C)	Ambient Temp. (C)	Diff. Temp. (C)
1	ACK60	37.45	36.34	-1.11	37.27	36.87	-0.40	35.22	35.94	0.72
2	AKS34	37.97	36.77	-1.20	37.03	36.77	-0.26	35.42	35.93	0.51
3	AKS35	37.05	36.10	-0.95	36.60	36.80	0.20	35.40	36.00	0.60
4	AKS36	37.22	35.24	-1.98	36.66	36.74	0.08	35.89	36.07	0.18
5	AKS37	37.63	36.72	-0.91	37.12	36.87	-0.25	34.76	35.89	1.13
6	AKS38	37.54	36.90	-0.64	36.97	36.93	-0.04	35.80	36.23	0.43
7	AKS39	38.14	36.31	-1.83	36.97	36.67	-0.30	35.74	36.10	0.36
8	A2TX398	38.12	36.97	-1.15	37.10	36.67	-0.43	35.82	36.07	0.25
9	A2TX2788	39.55	37.43	-2.12	37.47	36.64	-0.83	36.40	36.20	-0.20

climate was a result of the high plant and soil moisture contents. This highly available moisture reduced the air temperature around plants in the high soil moisture level plots through evaporative cooling. The evaporation of the available moisture cooled the surrounding air, which resulted in low ambient air temperature in those high soil moisture level plots. Leaf temperatures under high soil moisture levels were low because plants were able to cool themselves. Thus, low ambient air temperature which resulted from the effect of the microclimate and low leaf temperature made the temperature differential low under the high soil moisture level. On the other hand, the low soil moisture level (low water level) had not enough moisture to cool the surrounding air. By comparing the medium and high soil moisture levels, the lower differences between the two temperatures were obtained under the medium soil moisture stress, except for the last two lines, A<sub>2</sub>Tx 398 and A<sub>2</sub>Tx2788. The largest differences were under the soil moisture non-stress level (Table 7). These results are in agreement with Clarke and McCaig (1982b), who observed that in rape plants, numerical values for leaf temperature increased, becoming close to the ambient temperature as soil moisture stress increased.

Under medium soil moisture stress, the numerical values for temperature differential were intermediate between

high soil moisture stress and soil moisture non-stress (Table 7).

The temperature differential under the soil moisture non-stress level ranged from 0.25 for A<sub>2</sub>Tx398 to 1.13 °C for AKS37, except A<sub>2</sub>Tx2788, which has a negative value of -0.20 (Table 8). The medium soil moisture stress level temperature differential numerical values ranged from -0.38 to 0.20 °C. The high soil moisture stress level ranged from -2.12 to -0.64 °C.

Statistically, all lines responded equally under high soil moisture stress and under soil moisture non-stress. Under the medium soil moisture stress line, A<sub>2</sub>Tx2788 was not significant at the 5% level of probability (Table 8).

The ambient temperatures of all lines for all three soil moisture levels were within the optimum range of air temperatures for sorghum of 35 to 42 °C, as reported by Jordan and Sullivan (1982). The range in leaf temperatures of all lines among the three soil moisture levels was 34.77 to 39.55 °C. All leaf temperatures were essentially within the optimum range in air temperature for sorghum. The plant leaf temperatures did not rise greatly even under high soil moisture stress.

#### Leaf Temperature

There was very little variability for leaf temperature among all nine lines within all three levels of soil moisture

Table 8. Means of leaf temperature differential for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

	Lines	Temperature Differential (C°)		
		Soil Moisture Stress Levels		
		High	Medium	Non-stress
1	ACK60	-1.11 Y	-0.40 Y	0.72 Y
2	AKS34	-1.20 Y	-0.26 Y	0.51 Y
3	AKS35	-0.95 Y	0.20 Y	0.60 Y
4	AKS36	-1.98 Y	0.08 Y	0.18 Y
5	AKS37	-0.91 Y	-0.25 Y	1.13 Y
6	AKS38	-0.64 Y	-0.04 Y	0.43 Y
7	AKS39	-1.83 Y	-0.30 Y	0.36 Y
8	A <sub>2</sub> Tx398	-1.15 Y	-0.43 Y	0.25 Y
9	A <sub>2</sub> Tx2788	-2.12 Y	-0.83 N	-0.20 Y

<sup>1</sup> Values followed by (Y) letter in the same column are the best ones at 0.05 significant level (i.e., the probability of correct selection  $[P(\text{CS}) = (1 - \alpha)]$  is 95% according to Hsu's procedure for selecting the best treatment in a subset.

stress (Figure 6). Under the soil moisture non-stress and medium soil moisture stress, all of the lines were statistically similar at the 5% confidence level. Under high soil moisture stress, A<sub>2</sub>Tx2788 responded significantly different for leaf temperature from all the other eight lines with a high temperature of 39.55 °C (Table 9).

Medium and high soil moisture stresses elevated leaf temperatures over soil moisture non-stress for all lines. The increases in leaf temperatures from soil moisture stress varied among lines. Under medium soil moisture stress the percent of increase in leaf temperature over soil moisture non-stress ranged from 2.17% for AKS36 to 6.76% for AKS37. Under high soil moisture stress the temperature increases ranged from 3.73% for AKS36 to 8.65% for A<sub>2</sub>Tx2788.

Increased leaf temperature due to increases in soil moisture stress under medium and low water levels were associated with increases in diffusive resistance and decreases in photosynthesis and transpiration. This is in agreement with what had been reported by Idso et al., 1981; Miura, 1982, and Kannangara et al., 1983.

The variation in leaf temperature of the nine lines among the three soil moisture stress levels is due primarily to the effect of soil moisture stress. The ambient temperature ranged from 35.23 to 37.43°C (Table 7), which is within the optimum range for photosynthesis in sorghum of 35 to 42°C (Gerik, 1979; Jordan and Sullivan, 1982).

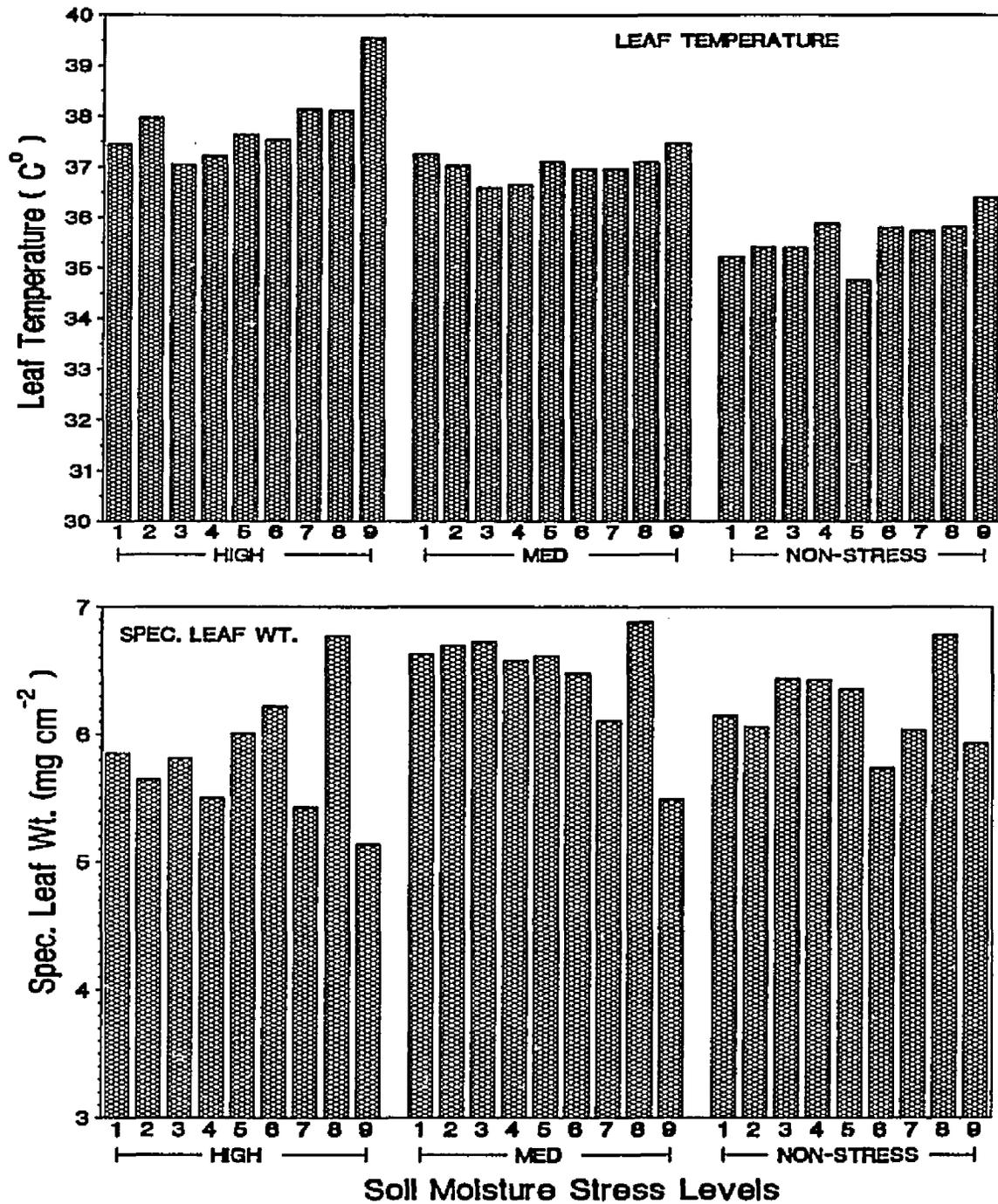


Fig.6. Mean responses of leaf temperature and specific leaf weight over 10 weeks after planting of nine sorghum lines grown under high, medium and non-stress soil moisture stress levels.<sup>1</sup>

1/ 1) ACK80      3) AKS35      5) AKS37      7) AKS39      9) A2TX2788  
 2) AKS34      4) AKS36      6) AKS38      8) A2TX398

Table 9. Means of leaf temperature for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

	Lines	Leaf Temperature Means (C°)		
		Soil Moisture Stress Levels		
		High	Medium	Non-stress
1	ACK 60	37.45 Y	37.27 Y	35.22 Y
2	AKS 34	37.97 Y	37.03 Y	35.42 Y
3	AKS 35	37.05 Y	36.60 Y	35.40 Y
4	AKS 36	37.22 Y	36.66 Y	35.88 Y
5	AKS 37	37.63 Y	37.12 Y	34.77 Y
6	AKS 38	37.53 Y	36.97 Y	35.80 Y
7	AKS 39	38.13 Y	36.97 Y	35.73 Y
8	A <sub>2</sub> TX398	38.12 Y	37.10 Y	35.82 Y
9	A <sub>2</sub> TX2788	39.55 N	37.47 Y	36.40 Y

<sup>1</sup> Values followed by (Y) letter in the same column are the best ones at 0.05 significant level (i.e., the probability of correct selection  $[P(\text{CS}) = (1 - \alpha)]$  is 95% according to Hsu's procedure for selecting the best treatment in a subset.

### Specific Leaf Weight

Specific leaf weight (SLW) of a plant is a measurement of the dry matter weight of a specific area of leaf. The specific leaf weight was calculated by dividing the dry leaf weight in mg of a piece of leaf by its area in  $\text{cm}^2$  as follows:

$$\text{SLW}(\text{mg cm}^{-2}) = \frac{\text{Dry leaf weight (mg)}}{\text{Leaf area (cm}^2\text{)}}$$

Specific leaf weight responded differently to soil moisture stress levels than did photosynthesis and transpiration.

The highest values of SLW were observed under medium soil moisture stress with generally lower values under soil moisture non-stress and lowest SLW values under high soil moisture stress (Table 10). A<sub>2</sub>Tx2788 was the only line that did not respond with highest SLW under medium soil moisture stress, but had its highest SLW under soil moisture non-stress. AKS38 was the only other line to respond differently to the three soil moisture levels by having its lowest SLW under soil moisture non-stress and its medium SLW under high soil moisture stress (Table 10).

The greater variability of responses for SLW of the nine lines to high soil moisture stress compared to less variability under soil moisture non-stress and least variability under medium soil moisture stress is illustrated in

Table 10. Means of specific leaf weight for nine sorghum lines grown under high, medium, and non-stress soil moisture stress levels.

	Lines	Specific Leaf Weight (mg cm <sup>-2</sup> ) Soil Moisture Stress Levels		
		High	Medium	Non-stress
1	ACK60	5.85 Y <sup>(1)</sup>	6.63 Y	6.15 Y
2	AKS34	5.65 N	6.69 Y	6.06 Y
3	AKS35	5.81 Y	6.72 Y	6.43 Y
4	AKS36	5.50 N	6.58 Y	6.43 Y
5	AKS37	6.01 Y	6.61 Y	6.36 Y
6	AKS38	6.22 Y	6.47 Y	5.74 N
7	AKS39	5.43 N	6.11 Y	6.03 N
8	A <sub>2</sub> Tx398	6.77 Y	6.88 Y	6.78 Y
9	A <sub>2</sub> Tx2788	5.13 N	5.49 N	5.93 N

<sup>1</sup> Values followed by (Y) letter in the same column are the best ones at 0.05 significant level (i.e., the probability of correct selection [P(CS) = (1 -  $\alpha$ )] is 95% according to Hsu's procedure for selecting the best treatment in a subset.

Figure 6. High soil moisture stress produced the lowest SLW for all lines, except AKS38, and the greatest variation among the lines. Soil moisture non-stress produced the medium SLW for all lines, except AKS38 and A<sub>2</sub>Tx2788, and a medium amount of variation among the lines (Figure 6).

All of the A<sub>1</sub> sterility type cytoplasm lines as a group had large differences in SLW among soil moisture levels. The A<sub>2</sub> sterility type cytoplasms exhibited smaller differences in SLW among the three soil moisture levels but with a considerable difference between the two A<sub>2</sub> cytoplasms within soil moisture levels. A<sub>2</sub>Tx398 had the highest SLW among all nine lines within each of the three soil moisture levels but with very little variation among soil moisture levels. The other A<sub>2</sub> cytoplasm, A<sub>2</sub>Tx2788 had the lowest SLW among all nine lines within the high and medium soil moisture stress levels and next to the lowest in the soil moisture non-stress level, with little variation among soil moisture levels. These differences between A<sub>1</sub> and A<sub>2</sub> sterility type cytoplasm suggest (1) that the A<sub>1</sub> is more sensitive to soil moisture stress levels for SLW than the A<sub>2</sub> sterility system cytoplasm and (2) that there is potential variation within the A<sub>2</sub> sterility system cytoplasm used in this experiment for levels of SLW.

There was a similarity of response to high soil moisture stress for high specific leaf weight, apparent photosynthesis and transpiration among the nine lines. AKS37,

AKS38 and A<sub>2</sub>Tx398, under high soil moisture stress, had the highest specific leaf weights (Table 10) and apparent photosynthesis (Table 3). AKS37 and AKS38, under high soil moisture stress, had also the highest transpiration rates of all nine lines, with A<sub>2</sub>Tx398 as fourth highest in transpiration rate. These results indicated a positive interrelationship among specific leaf weight, rate of photosynthesis and transpiration rate under the high soil moisture stress imposed in this experiment.

Smith and Nobel (1978) reported that soil moisture stress at the time of leaf expansion reduces cell size, which leads to a smaller leaf area occupied by the same mass of cells or a greater number of cells per same unit of leaf area.

There are several plant growth activities that are affected by soil moisture stress. Cell division and cell growth are hindered by soil moisture stress. Cells are composed of carbohydrates, which are produced through photosynthesis, which in turn is slowed by soil moisture stress. Carbohydrate is a component of SLW. Salisbury and Ross (1985) reported that soil moisture stress decreases cell growth, reduces cell wall synthesis, protein synthesis, and some enzyme activities and inhibits cell division. These plant growth activities are not likely to be affected equally by specific levels of soil moisture stress.

The scope of this research did not encompass study of rates of cell division, cell growth and cell composition under various soil moisture stress levels.

It was observed that medium soil moisture stress produced higher SLW than the soil moisture non-stress condition. Perhaps cells were smaller under medium soil moisture stress but with equal amount of carbohydrate structure as soil moisture non-stress, thus giving higher SLW. As soil moisture stress became more severe, photosynthesis then slowed carbohydrate production sufficiently to cause small cells with a light structure producing a very low SLW, especially in the vegetative stage of sorghum entries in this experiment.

## SUMMARY AND CONCLUSIONS

Seven sorghum cytoplasms represented by nine lines were evaluated under three levels of soil moisture stress under a single line irrigation gradient system. The plant characteristics studied were apparent leaf photosynthesis, transpiration rate, diffusive resistance, temperature differential, leaf temperature, and specific leaf weight.

Leaf photosynthesis responses to the three soil moisture levels indicated that there were greater differences among cytoplasms for rate of leaf photosynthesis at the high and low soil moisture stress levels, and least differences under the medium soil moisture stress level. Under high soil moisture stress, three lines AKS37, AKS38, and A<sub>2</sub>Tx398 had significantly higher rates of photosynthesis than the other six. These three entries also maintained high specific leaf weights, high transpiration rates, and low diffusive resistance values under high soil moisture stress.

Lines A<sub>2</sub>Tx398 and A<sub>2</sub>Tx2788 under soil moisture non-stress had significantly lower rates of leaf photosynthesis than the other seven lines. There were no significant differences among all nine lines under soil moisture non-stress for transpiration and diffusive resistance.

There were no significant differences among all nine lines under medium soil moisture stress for leaf photosynthesis, transpiration and diffusive resistance.

Differences in leaf temperature among the three soil moisture levels for each of all nine lines decreased in value with increased soil moisture (decreased soil moisture stress).

The differences in values of the ambient temperature minus leaf temperature (leaf temperature differential) among the three soil moisture levels for each of the nine lines decreased from high negative numerical values as soil moisture increased (decreased soil moisture stress). The high soil moisture level (soil moisture non-stress) resulted in mostly all positive leaf temperature differential values.

Specific leaf weight was, except for one line, highest under medium soil moisture stress and lower under both high soil moisture stress and soil moisture non-stress.

This research suggests that the differences in leaf photosynthesis among the lines to soil moisture stress levels were related, in some cases, to differences in cytoplasm where lines had the same genomes. In other cases of similar cytoplasm but different genomes, some traditional variable nuclear control of photosynthesis may also exist.

Three lines AKS37, AKS38 and A<sub>2</sub>Tx398 had significantly higher rates of leaf photosynthesis under high soil moisture

stress than the other six lines, and were thus considered to be soil moisture stress tolerant. These high leaf photosynthesis rates were accompanied with high specific leaf weights, high transpiration rates, and low diffusive resistance values. Line A<sub>2</sub>Tx398 may be considered to be the more moisture stress tolerant of the three due to its lower transpiration rate. The other two lines, AKS37 and AKS38, are considered statistically to be substitutes for A<sub>2</sub>Tx398 in terms of soil moisture stress tolerance. The other six lines evaluated in this research may be considered to be susceptible to soil moisture stress.

The results of this research indicate that there are five different source areas of variation in rates of photosynthesis performance under soil moisture stresses. These areas are among and within cytoplasm types, from which germplasm may be selected, as follows:

1. Photosynthesis variation among cytoplasms of different sorghum species.
2. Photosynthesis variation within cytoplasms of different sorghum species.
3. Photosynthesis variation among cytoplasmic-genic sterility types within a species.
4. Photosynthesis variation within cytoplasmic-genic sterility types within a species.

5. Stability of photosynthesis across levels of soil moisture from non-stress to stress within cytoplasmic-genic sterility types within a species.

APPENDIX A

RESPONSE OF PHOTOSYNTHESIS TO REWATERING  
OF NINE SORGHUM LINES GROWN UNDER  
HIGH SOIL MOISTURE STRESS

Table A. Response of photosynthesis to rewatering of nine sorghum lines grown under high soil moisture stress.<sup>1</sup>

Variable	Weeks After Planting	Lines								
		1	2	3	4	5	6	7	8	9
Total water applied each time (cm)	8	2.37	2.27	2.36	2.39	2.64	2.67	2.61	2.73	2.60
Apparent PS		10.503	13.238	12.196	9.125	22.611	24.904	8.618	24.084	15.288
Total water applied each time (cm)	9	0.94	0.84	0.94	0.95	1.08	1.13	1.09	1.13	1.08
Apparent PS		4.381	4.541	5.329	0.293	9.779	10.680	6.610	7.791	11.291
Total water applied each time (cm)	10	1.07	1.00	1.08	1.02	1.23	1.24	1.16	1.26	1.21
Apparent PS		9.572	6.340	8.353	8.280	17.428	17.66	10.876	20.356	2.229
Total water applied each time (cm)	11	3.51	3.52	3.45	3.54	3.53	3.500	3.63	3.61	3.55
Apparent PS		25.190	19.139	18.518	23.056	22.044	23.860	25.394	26.907	14.007

<sup>1/</sup> 30 cm of water applied by using furrow irrigation throughout the 39 days from the beginning of the season before plants were subjected to water stress. The water received during the last seven days was mainly from rainfall.

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