TITLE

Effects of Heat and Water Stress and Their Interactions on

Grain Sorghum [Sorghum bicolor (L.) Moench]

BY

Baba Kura Kaigama

APPROVED	DATE
Charles J. Sullivan	June 3, 1982
Maxwell Clegg	June 3, 1982
John M Norman	June 3, 1982
R. E. Neil	6/3/82

SUPERVISORY COMMITTEE

GRADUATE COLLEGE

UNIVERSITY OF NEBRASKA

EFFECTS OF HEAT AND WATER STRESS

AND THEIR INTERACTIONS

ON GRAIN SORGHUM [Sorghum bicolor (L.) Moench]

Baba Kura Kaigama, Ph. D.

University of Nebraska, 1982

Adviser: Charles Y. Sullivan

A series of experiments were conducted to evaluate the interactions of water stress and high temperatures on the growth and development of grain sorghum [Sorghum bicolor (L.) Moench]. Effects of combinations of water stress and high temperatures on intact plants and of heat and desiccation on cut leaf tissue were also examined.

Potted plants were grown in temperature controlled greenhouses. Water stress reduced leaf emergence rates and the final leaf area while elevated temperatures, under non water stressed conditions and under mild water stress, enhanced leaf emergence rates and increased leaf area. When plants were well watered or only mildly water stressed, exposure to temperatures of 35 C during panicle development resulted in higher grain yields, but under 8 and 12 days of water stress plants grown in a 30 C environment gave higher yields. Elevated temperatures during boot stage reduced panicle weight, seed numbers, and grain yield, possibly due to floret abortion.

Leaf photosynthetic rates were greater for plants that had been water stressed at -0.3 and -0.45 MPa than for the controls, but dry matter accumulation rates were greater for the controls. Exposure to temperatures of 38 C increased photosynthetic rates but 40 C caused photosynthetic rates to decline.

Under non water stressed conditions, exposure to elevated tempera-

tures hastened bloom and physiological maturity but bloom was delayed when elevated temperatures were coupled with water stress. Eight and 12 days without irrigation delayed bloom by 2 to 9 days, and physiological maturity by 3 to 12 days.

Eight and 12 days without irrigation induced tillering in plants grown in a 30 C environment but even 4 days without irrigation induced tillering in plants grown under 35 C.

Both water stress and elevated temperatures increased heat and desiccation tolerance of sorghum leaf tissue. There were genotypic differences in the degree of heat and desiccation tolerance but these differences disappeared with plant age, with increased water stress, and with extended exposure to elevated temperatures.

Significant interactions between water stress and temperature were observed with 4 to 12 days of water stress, but not when osmotically controlled water stress levels were -0.3 to -0.6 MPa. Under well watered conditions and under 4 days of water stress, elevated temperatures accelerated plant growth and increased grain yield and total dry matter. When water stress periods were 8 or 12 days, elevated temperatures delayed plant development and reduced grain yield and total dry matter.

EFFECTS OF HEAT AND WATER STRESS AND THEIR INTERACTIONS ON GRAIN SORGHUM [*sorghum bicolor* (L.) Moench]

by

Baba K. Kaigama

A DISSERTATION

Presented to the Faculty of

The Graduate College in the University of Nebraska

In Partial Fulfillment of Requirements

For the Degree of Doctor of Philosophy

Major: Agronomy

Under the Supervision of Professor Charles Y. Sullivan

Lincoln, Nebraska

June, 1982

DEDICATION

To my parents

Alhaji Kaigama Mustafa and Hajja Aisa

ACKNOWLEDGEMENTS

I wish to express my most profound gratitude to Dr. Charles Y. Sullivan for his encouragement, support and guidance throughout the course of my program. I wish to sincerely thank Drs. Max D. Clegg and John M. Norman for accepting to serve on the supervisory committee and for a most helpful critique of the entire manuscript. Gratitude is also extended to Dr. Ralph E. Neild for serving on the supervisory committee.

My most sincere thanks to Miss Carol Caha for her assistance during every facet of this project. Thanks are also extended to Mr. James Harcourt without whose valuable assistance most of the controlled environmental studies would not have been possible. I also wish to thank all the professors, staff and students of the sorghum physiology group for their encouragement and support during the course of my program.

I wish to thank Ahmadu Bello University, Zaria, Nigeria and Borno State Government of Nigeria for financing my studies and the University of Nebraska, Lincoln, and the United States Department of Agriculture for providing the research facilities and equipment.

Thanks are due to Mrs. Blythe Stickney for an excellent job of typing the manuscript.

Last but by no means the least, I wish to thank my wife Kolo and my daughter Aishetu for their patience and support throughout my studies.

B.K.K.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
LITERATURE REVIEW	3
Sensitivity to Stress at Various Stages of Growth	3
Leaf Expansion	6
Photosynthesis and Respiration	7
Yield and Yield Components	12
Genotypic Differences in Response to Stress	18
MATERIALS AND METHODS	24
EXPERIMENT 1	24
Water and Temperature Stress Treatments	24
Genotypes	26
Cultural Practices	26
Observations, Measurements and Tests	28
EXPERIMENT 2	30
EXPERIMENT 3	34
Water and Temperature Stress Treatments	34
Preparation of Pots for Plant Growth in Nutrient Culture	36
Genotypes	36
Observations and Measurements	38
EXPERIMENT 4	39
Treatments	39
Measurements	39
EXPERIMENT 5	41
Treatments	41
Application of Treatments	41
Genotypes	43
Measurements	45
EXPERIMENT 6	47
Treatments	47
Measurements	47

Page

EXPERIMENT 7. 51

Treatments 51
Measurements 51

RESULTS AND DISCUSSION 54

EXPERIMENT 1. 54

Leaf Emergence Rate. 54
Reproductive Development 56
Tillering. 60
Plant Height 62
Yield and Yield Components 66
Panicle Size. 66
Seed Numbers. 70
Seed Size 75
Grain Yield 81
Leaf Dry Matter. 86
Stem Dry Matter. 86
Total Dry Matter 86
Interactions of Environment, Water Stress and Genotype . 94
Environment x Water Stress. 94
Environment x Genotype. 96
Water Stress x Genotype 97
Environment x Water Stress x Genotype 97
Heat and Desiccation Tolerance Tests 97

EXPERIMENT 2. 113

Preliminary Tests. 113
Genotype B (Martin x SC33-9-2-2-2) 116
Genotype Martin B. 118

EXPERIMENT 3. 120

Leaf Emergence Rate. 120
Reproductive Development 123
Yield and Yield Components 125
Panicle Weight. 125
Number of Seeds 127
Seed Size 130
Grain Yield 132
Other Plant Parts. 132
Interactions of Water Stress and Temperature 137

EXPERIMENT 4. 138

Page

EXPERIMENT 5 144

Leaf Expansion. 144
Photosynthesis. 149
Dry Matter Accumulation 153

EXPERIMENT 6 156

Leaf Expansion. 156
Photosynthesis. 159
Dry Matter Accumulation 164

EXPERIMENT 7 166

Leaf Development. 166
Plant Dry Matter. 174
Interactions of Water Stress and Temperature. 176

SUMMARY 177

LITERATURE CITED. 185

APPENDIX. 195

LIST OF TABLES

Table		Page
1	Description of environments and genotypes for experiment 1 .	25
2	Nutrient solution for experiments 1 and 2.	27
3	Nutrient solution for experiments 3 to 7	35
4	Description of treatment combinations for experiment 5 . . .	42
5	Description of treatment combinations for experiment 6 . . .	48
6	Ten-day averages of minimum, maximum, and weighted average temperatures (C) for the 4 environments in experiment 1. . .	55
7	Lengths and widths (cm) and length x width (cm^2) of leaves 5 and 8 measured before water stress was imposed on four sorghum hybrids grown under two temperature environments . .	57
8	Days from emergence to half-bloom and to physiological maturity for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	59
9	Average tiller weights (g per plant) for four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	61
10	Plant height (cm) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.	63
10a	Plant height expressed as percentages of genotype A, water stress 0, environment 1.	64
11	Panicle weight (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	67
11a	Panicle weight per plant expressed as percentages of genotype A, water stress 0, enviroment 1	68
12	Number of seeds per plant for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	71

Table		Page
12a	Number of seeds per plant expressed as percentages of genotype A, water stress 0, environment 1.	72
13	Weight of 1000 seeds (g) for 4 sorghum hybrids grown under four temperature environments and subjected to 2 cycles of 0, 4, 8, and 12 days of water stress	76
13a	Weight of 1000 seeds expressed as percentages of genotype A, water stress 0, environment 1.	77
14	Grain yield per plant (g) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	82
14a	Grain yield per plant expressed as percentages of genotype A, water stress 0, environment 1.	83
15	Leaf dry matter (g per plant) for four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress. . . .	87
15a	Leaf dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1.	88
16	Stem dry matter (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress	89
16a	Stem dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1, ...	90
17	Total dry matter (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress. . . .	91
17a	Total dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1.	92
18	Interactions between environment, water stress, and genotype for the various plant parameters measured in experiment 1	95
19	Percentage injury to leaf discs of control and mildly water stressed plants sampled 45 days after emergence and heated at 53.5 C	99

Table		Page
19a	Percentage injury to leaf discs of control and mildly water stressed plants sampled 45 days after emergence and desiccated at - 16 bars (-1.6 Mpa) with PEG.	100
20	Percentage injury to leaf discs of control and moderately water stressed plants sampled 49 days after emergence and desiccated at -16 bars (-1.6 MPa) with PEG	102
21	Percentage injury to leaf discs of control and severely water stressed plants sampled 56 days after emergence and heated at 53.5 C	104
21a	Percentage injury to leaf discs of control and severely water stressed plants sampled 56 days after emergence and desiccated at -16 bars (-1.6 MPa) with PEG	105
22	Percentage injury to leaf discs of control and mildly water stressed plants sampled 68 days after emergence and heated at 53.5 C	107
23	Percentage injury to leaf discs of control and moderately water stressed plants sampled 75 days after emergence and heated at 53.5 C	108
24	Percentage injury to leaf discs of control and severely water stressed plants sampled 81 days after emergence and heated at 53.5 C	109
25a	Effect of heating at various temperatures or desiccation with various concentrations of PEG 600 on percentage injury to leaf discs of three sorghum genotypes taken 65 days after emergence.	114
25b	Effect of leaf position on percentage injury to leaf discs of sorghum genotype 226 taken 65 days after emergence and heated at 53.5 C	114
25c	Effect of heating with and without water and the length of the holding period in the cold room on percentage injury to leaf discs of sorghum genotype 226 taken 70 days after emergence.	115
25d	Effect of heating temperature and the length of the holding period in the cold room on percentage injury to leaf discs of sorghum genotype Martin B taken 76 days after emergence	115

Table		Page
26	Effect of various combinations of heat and desiccation treatments on percent injury to leaf discs of sorghum genotypes B and Martin B taken 72 and 76 days after emergence, respectively.	117
27	Ten-day averages of maximum, minimum, and weighted average temperatures (C) for the two environments in experiment 3	121
28	Average number of fully expanded leaves on various days after emergence for three sorghum hybrids grown under two temperature environments	124
29	Number of days from emergence to half-bloom for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	126
29a	Number of days from emergence to physiological maturity for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress	126
30	Panicle weight (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	128
31	Number of seeds per plant for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	129
32	Weight of 1000 seeds (g) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress	131
33	Grain yield (g per plant) for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	133
34	Leaf dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	134
35	Stem dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	135

Table		Page
36	Root dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.	136
37	Regression equations and estimates of leaf area from the product of leaf lengths and widths for three sorghum hybrids.	139
37a	Ratio of actual leaf area to the product of leaf length and width for three sorghum hybrids	141
38	Dry matter, water use efficiency, and area of leaf 5 for three sorghum hybrids grown under two temperature environments.	142
39	Regression equations developed from measurements of leaf length, leaf width, and actual leaf area for three sorghum genotypes.	146
39a	Ratio of actual leaf area to the product of leaf length and leaf width for various leaves of three sorghum genotypes.	146
40	Area of leaves 5 and 6 (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	148
41	Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 18 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	150
41a	Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 24 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	152
42	Dry matter accumulation rates (mg per day) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. . . .	154
43	Cumulative leaf area (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.	158

Table		Page
44	Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 18 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	160
44a	Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 25 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	162
45	Dry matter accumulation rates (mg per day) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. . . .	165
46	Day and night temperatures (C) and relative humidity (%) in the four environments of experiment 7 averaged over varying numbers of days after emergence	167
47a	Area of leaves fully expanded (cm^2) before various levels of water stress were imposed on three sorghum genotypes grown under four temperature environments.	169
47b	Area of leaves fully expanded (cm^2) during the water stress period for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	170
47c	Ratio of leaf area expanded during the water stress period to leaf area expanded up to the end of the water stress period for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress	172
47d	Total cumulative leaf area (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.	173
48	Total dry matter (g per plant) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.	175

LIST OF FIGURES

Figure		Page
1	Aeration system for plant growth in nutrient culture	37
2	Summary of temperature and water stress treatments for experiment 5	44
3	Summary of temperature and water stress treatments for experiment 6	49
4	Summary of temperature and water stress treatments for experiment 7	52
5	Plant height (cm) of 4 sorghum hybrids plotted against days of water stress by environments	65
6	Panicle weight (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments	69
7	Number of seeds per plant for four sorghum hybrids plotted against days of water stress by environments	74
8	Weight of 1000 seeds (g) of 4 sorghum hybrids plotted against days of water stress by environments	79
9	Grain yield (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments	85
10	Total dry matter (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments	93
11	Percentage injury to sorghum leaf discs versus cumulative growing degree days for control and 4 days water stressed plants sampled 68 days after emergence. Treatment temperature was 53.5 C for 15 minutes	111
12	Percentage injury to sorghum leaf discs versus cumulative growing degree days for control and 8 days water stressed plants sampled 75 days after emergence. Treatment temperature was 53.5 C for 15 minutes	112
13	Averages of periodic measurements of percent relative humidity plotted against time of day for the two environments of experiment 3	122

Figure | Page

14 Relative humidity (%) and temperature (C) in the two controlled environmental chambers of experiment 5 during one 24-hour period 145

15 Relative humidity (%) and temperature (C) in the two controlled environmental chambers of experiment 6 averaged over a 5-day period 157

16 Concentrations of CO_2 in air (ppm) going into and coming out of the two controlled environmental chambers of experiment 6 plotted against time of day on May 5, 1981 163

LIST OF APPENDIX TABLES

Table		Page
A1	Directions for preparing HEDTA-Fe	196
A2	Procedure for heat tolerance test	197
A3	Procedure for desiccation tolerance test.	198
A4	Dry matter (g per plant) at 19 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 5)	199
A5	Dry matter (g per plant) at 27 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 5)	200
A6	Dry matter (g per plant) at 19 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 6)	201
A7	Dry matter (g per plant) at 26 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 6)	202
A8.1	Mean squares for plant height, leaf dry matter, stem dry matter, and total dry matter of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress. (Experiment 1).	203
A8.2	Mean squares for panicle weight, number of seeds, and grain yield of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress. (Experiment 1). .	204
A8.3	Mean squares for weight of 1000 seeds of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress. (Experiment 1)	205

Table		Page
A9.1	Mean squares for leaf dry matter, stem dry matter, and root dry matter of three sorghum hybrids grown under two temperature environments and subjected to 0, -4, and -6 bars of water stress. (Experiment 3). . . .	206
A9.2	Mean squares for panicle weight, number of seeds, and grain yield of three sorghum hybrids grown under two temperature environments and subjected to 0, -4, and -6 bars of water stress. (Experiment 3)	207
A10.1	Mean squares for top dry matter, root dry matter, and total dry matter of three sorghum hybrids grown under two temperature environments. (Experiment 4). . . .	208
A10.2	Mean squares for total water use, water use efficiency, and area of the 5th leaf of three sorghum hybrids grown under two temperature environments. (Experiment 4)	209
A11.1	Mean squares for leaf area and dry matter accumulation rates for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 5)	210
A11.2	Mean squares for net photosynthetic rates measured 14 days after relief of water stress for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 5)	211
A12.1	Mean squares for cumulative leaf area and dry matter accumulation rates of three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 6). . .	212
A12.2	Mean squares for net photosynthetic rates measured 13 days after relief of water stress for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 6)	213
A13	Mean squares for leaf area and total dry matter of three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 7)	214

INTRODUCTION

Countless experiments have been conducted and many reviews written on the effects of water and high temperature stress on various physiological and agronomic aspects of crop plants, and it is very well established that both types of stress affect many important physiological and morphological aspects of plants. Water stress causes plant water deficits that reduce cell turgor, causing stomatal closure and reduction in cell enlargement. This reduces leaf surface area and the rate of photosynthesis and thus inhibits growth. High temperature increases water loss and the utilization of metabolites in respiration. Levitt (1980) gave two reasons for increased water loss with rise in temperature of the environment: (1) the direct effect of temperature on the diffusion constant of water and (2) the steepening of the vapor pressure gradient between the leaf and the external atmosphere. Apart from the increased water loss it is becoming increasingly evident that direct high temperature injury to field grown crops does occur (Sullivan and Ross, 1979). Bjorkman et al. (1980) reported that photosynthesis in two desert species was completely inactivated before other high temperature injury symptoms could be detected. They considered this to be an indication that the observed thermal inactivation of photosynthesis was caused primarily by a direct effect of temperature on the photosynthetic machinery itself. Raison et al. (1980) also

suggested that many of the high temperature induced effects that have been described in plants may be directly related to a perturbation of membrane structure and function by heat.

Through their effects on various plant processes water stress and high temperature stress often limit the genetic potential of crop plants. The degree of injury from water or high temperature stress depends on a number of factors including the duration of exposure to stress conditions, the adaptation of the particular cultivar or species, and the stage of growth at which stress is imposed. Other factors include the extent of prior hardening that may have occurred and the level of irradiance.

It is often difficult to separate the effects of water stress from those imposed by high temperature, because in the field high temperatures often accompany periods of water deficit and the two components are inevitably confounded. Despite their importance in determining production of crops no detailed examination of the interactions of water stress and high temperature appears to have been made.

The study reported here was designed as an attempt to delineate some of the interactions between water and high temperature stress on the growth and yield and some physiological processes of grain sorghum (Sorghum bicolor L. Moench) and to look at the effects of the two stresses applied together as compared to one stress preceeding or immediately following the other.

LITERATURE REVIEW

Sensitivity to Stress at Various Stages of Growth

Salter and Goode (1967) have summarized evidence which demonstrates that the extent of yield reduction from water deficits depends on the stage of plant growth, among other factors. Hughes et al. (1959) found that water stress at any stage of development reduced grain sorghum yields but particularly so at the early bloom and soft dough stages. Lewis et al. (1974) on the other hand, reported a greater reduction in grain yield when stress was imposed during boot to bloom than during either late vegetative to boot or milk through soft dough stages in sorghum subjected to -12 to -13 bars of soil water stress. Irrigated grain sorghum subjected to various periods of plant water stress at boot, head emergence, and early grain filling showed various degrees of reduction in grain yield depending on the length of the stress period and the stage of growth of the crop (Eck and Musick, 1979a). In agreement with Lewis et al. (1974), greater reductions in yield were observed when stress occurred at early boot or head emergence than at early grain filling.

Nour et al. (1978) evaluated 10 sorghum cultivars for drought resistance by subjecting 9-day old seedlings to four successive cycles of water stress. After the fourth cycle, cultivars known to have the highest resistance had the highest survival rate. Others (Kilen and Andrew, 1969; Williams et al.,

1969) have found that seedling drought resistance does not necessarily correlate with that at older stages of development.

Shipley and Regier (1970) reported the failure of parts of heads of RS 671 to emerge from boots when stress developed during the boot stage. In the study by Eck and Musick (1979a), moderate stress during boot shortened the peduncles of Pioneer 8311 but complete heads were exerted.

Eck and Musick (1979b) reported greater reductions in total dry matter accumulation when stress was initiated at early boot than when it was initiated at head emergence or early grain filling. Of three growth stages tested, the greatest reduction in grain yield of sorghum was when water stress occurred at the boot stage (Inuyama, 1978b). Wilson et al. (1980) also reported reduction in dry matter when grain sorghum cv. RS 610 at the eight-leaf stage was subjected to water stress. This reduction was attributed to a reduction in leaf area index and a decrease in substrate production rate per unit of leaf area by photosynthesis. Claassen and Shaw (1970) reported a significant (12-15%) reduction in grain yield of maize (Zea mays L.) subjected to water stress during early ear shoot and ovule development as compared to a 53% reduction associated with stress at 75% silking and a 30% reduction associated with a three-week post silking period. Water stress during meiosis in maize stunted growth and tassel development and reduced chlorophyll content and light

absorption but was not detrimental to yield (Downey, 1971). Drought stress during grain filling reduced grain yield by 50%. Wilson and Allison (1978) reported a decrease in the rate of growth of stem, root, leaf, and ear, and increased leaf senescence and retarded silk growth in corn subjected to mild water stress during the period of ear development before flowering. This decreased the grain capacity of the plants to store all the dry matter produced after flowering when the plants were well watered, and the surplus was stored mainly in the stem.

In an experiment designed to determine the effect of temperature on the development of water stress and subsequent recovery in spring wheat (Triticum aestivum L.), Frank et al. (1973) reported that stomatal closure occurred at -13, -13, and -15 bars of leaf water potential at tillering and at -18, -17, and -26 bars at head emergence for plants grown at temperatures (both day and night) of 10, 18, and 27 C, respectively. They further reported that in non-water stressed plants temperature greatly influenced leaf water potential.

Stout (1977) reported that growth occurred in two sorghum cultivars during water stress but at a reduced rate. Water stress shortened leaf and stem growth period and advanced inflorescence development in the cultivar NK300 while it extended the period of leaf and stem growth and delayed inflorescence development in the cultivar M35. This may have been due to the shorter life cycle of NK300 compared to M35.

Leaf Expansion

Since crop evaporation is linearly related to leaf area until complete ground cover (Ritchie, 1974), a reduction in leaf area before complete cover will reduce water loss. Leaf expansion is one of the most sensitive processes to water stress (Acevedo et al., 1971; Boyer, 1970a; Boyer, 1976; Hsiao et al., 1970) and even short periods of water stress in the vegetative stage can have permanent effects on the final leaf area achieved by crops (Acevedo et al., 1971; Boyer, 1970a; Ludlow and Ng, 1977). Differences in the sensitivity of leaf expansion to water stress has been observed between species (Turner and Begg, 1978), but has not been measured among cultivars.

Leaf elongation rates in wheat, rye grass (Lolium perenne L.), and maize were found to be strongly affected by water stress of less than -5 bars plant water potential (Penning de Vries et al., 1979). Sharp et al. (1979) reported an appreciable reduction in the rate of leaf expansion in both corn and sorghum when water was withheld for three days. Boyer (1970a) reported that leaf elongation in corn and enlargement in soybeans (Glycine max L.) and sunflower (Helianthus annus L.) approached zero at leaf water potentials of -9, -12.5, and -4 bars, respectively. McCree and Davies (1974) looked at the effect on sorghum leaf expansion, of a warm moist environment, a hot dry environment, and a hot dry environment in which plants were subjected to five cycles of water stress.

Both the rate of increase in leaf area and the final leaf area declined progressively from the warm moist environment to the hot dry environment coupled with five cycles of water stress.

Watts (1972a) reported that air temperature appeared to exert a strong influence on corn leaf extension independently of the water status of the leaf. Watts (1972b) further reported that when air temperature and vapor pressure deficit were high enough transpiration was so fast that water loss exceeded water uptake to such an extent that the water potential of leaf tissue decreased and leaves extended more slowly. Downes (1968) reported that the rate of leaf appearance for Combine Kafir sorghum increased linearly with average daily temperature between 13 and 23 C. The maximum leaf elongation rate occurred at 30/25 C (day/night) temperature. Tollenaar et al. (1979) reported the same linear relationship between the rate of corn leaf appearance and temperature, between 10 and 30 C.

In addition to their effect on leaf size, water or high temperature stress can also affect leaf area through their effect in hastening the rate of leaf senescence (Boyer, 1976; Fischer, 1973; Fischer and Hagan, 1965; Fischer and Kohn, 1966).

Photosynthesis and Respiration

Throughout the early growth stages of cereal crops the leaf blades are the main photosynthetic organs and crop growth

rate depends on both the rate of expansion of leaf area and the rate of photosynthesis per unit leaf area. In general, net photosynthesis is progressively reduced by water stress and negative values may develop when stress is severe (El-Sharkawy and Hesketh, 1964; Slatyer, 1967). Wien et al. (1979) reported that gas exchange measurements indicated that the photosynthetic mechanism was not severely impaired by water stress but cautioned that the extent of reduction in photosynthetic rate may have been underestimated as the leaf chamber temperature of 31 C was lower than the stressed leaf would experience in the field. Downes (1971) reported that photosynthesis in sorghum was not much modified by temperature between 25 and 35 C. Photosynthesis in sudan grass (Sorghum sudanense Stapf.) was also independent of temperature under low irradiance, but otherwise increased with temperature until a plateau was reached at about 30 C (Downes, 1970). Chrelashvili (1941) reported that a certain degree of mild water stress, the degree varying among species, caused CO_2 uptake to be at a maximum and then decreased after that point. Initial decreases in photosynthetic activity with water stress have generally been attributed to stomatal closure (Boyer, 1970b; Boyer, 1976; El-Sharkawy and Hesketh, 1964; Frank et al., 1973; Slatyer, 1967) but prolonged and severe water stress can lead to depression of chloroplast and enzyme activity and to nonstomatal effects on photosynthesis (Boyer, 1976; Boyer and Bowen, 1970; Boyer and Potter, 1973; Doley and Trivett, 1974; Giles et al.,

1976; Heichel and Musgrave, 1970; Keck and Boyer, 1974; Potter and Boyer, 1973; Redshaw and Meidner, 1972; Sullivan and Eastin, 1974), although several of the enzymes of the photosynthetic complex seem to be rather resistant to water stress (Huffaker et al., 1970; Santarius, 1967; Shearman et al., 1972; Sullivan and Eastin, 1969). Physical symptoms of stress appear long after considerable photosynthetic activity has been lost (Boyer and McPherson, 1975).

Net photosynthesis could decrease due to either a direct decrease in gross photosynthesis or a relatively greater decrease in gross photosynthesis as compared to dark respiration. Continued respiration after photosynthesis has slowed down or ceased, uses up stored foods, reduces substrate supply and hinders growth.

Brown and Thomas (1980) compared the respiration rates of individual leaves of sorghum, cotton (Gossypium hirsutum L.) and beans (Phaseolus vulgaris L.) which had been fully expanded prior to a series of severe water stresses with those of unstressed leaves of similar age. The respiration rates per unit leaf area of all rewatered plants were significantly lower than those of the plants which had not undergone water stress. Photosynthesis and respiration in tomatoes (Lycopersicon esculentum) were unchanged until leaf water potentials fell below -9 bars, but at -14 bars net photosynthesis was zero while dark respiration was depressed only 30% (Brix, 1962). Sung and Krieg (1979) reported a decline in photo-

synthetic rates as midday leaf water potentials declined from -14 to -27 bars in both cotton and sorghum, but photosynthesis was not completely inhibited in either species even at leaf water potentials of -27 bars. Boyer (1970a) observed that as leaf water potentials decreased photosynthesis was inhibited later and less severely than was leaf enlargement, and respiration was inhibited even less than photosynthesis. Norcio and Sullivan (1976) reported that differences in photosynthetic rates of two sorghum hybrids and their parents could be explained either by the direct effect of high temperature on the photochemical apparatus or by decreased leaf conductance. Plants that were heat treated acquired some hardening and were more resistant to thermal inactivation than the controls. Bjorkman et al. (1980) presented evidence to support that a greatly increased thermal stability of chloroplast membrane reactions plays a key role in the superior performance of one of two desert species at high temperatures. Alexandrov (1964) also concluded that the photosynthetic process is sensitive to high temperature. Frank et al. (1973) looked at the effect of temperature on the development of water stress and subsequent recovery in spring wheat. They observed that recovery of photosynthesis was related to the recovery of stomatal diffusion resistance, except that photosynthesis never fully recovered to prestress levels. Blum and Sullivan (1972) subjected two sorghum genotypes to leaf water stress by varying the % relative humidity of air circulating over excised leaf

sections. The effect of relative humidity on net photosynthesis was found to be dependent on incident radiation, with high incident irradiance intensifying the effect of lowered relative humidity, and increased vapor pressure deficits, on net photosynthesis reduction. Pasternak and Wilson (1976) reported that photosynthesis in sorghum leaves virtually ceased but continued at the same rate in the heads when water was withheld for seven days. Turner et al. (1978) on the other hand found that water deficits down to -1.4 MPa (-14 bars) and values of relative water content down to 93% in sorghum and 84% in soybeans had no apparent influence on leaf conductivity or $^{14}CO_2$ photosynthesis. They also stated, however, that values of leaf water potential sufficient to initiate stomatal closure and reduce photosynthesis were reached even in wet soil when the evaporative demand was high. Some of the differences in the response of photosynthesis to stress may be due to differences in the rate of development of stress as Jones and Rawson (1979) showed that sorghum plants allowed to dry slowly and adjust osmotically maintained a higher rate of photosynthesis at low leaf water potentials than sorghum plants in which little adjustment occurred. Fereres et al. (1978) observed no stomatal closure in sorghum even at leaf water potentials of -20 bars when soil water depletion occurred slowly. When water stress was made to develop much faster, stomata closed at -14 to -16 bars.

Growth under high temperature or high light intensity

increased the subsequent photosynthetic rate in maize (Hesketh, 1968). Light and temperature conditions during development may thus influence the subsequent photosynthetic capacity of leaves.

Yield and Yield Components

Vanderlip and Reeves (1972) identified ten stages of growth for grain sorghum beginning from stage 0 (emergence) to stage 9 (physiological maturity). Eastin (1972) divided the grain sorghum life cycle into three developmental stages: GS1 - planting to panicle initiation; GS2 - panicle initiation to bloom; and GS3 - bloom to physiological maturity.

GS1 is the vegetative phase when sufficient leaf area and root system is established to support later development. Panicle initiation and expansion occur during GS2 and the potential seed number is thus set during this developmental phase. GS3 is the grain filling phase and the length of time spent in this phase, or efficiency of filling rate largely determines the potential seed size.

Control of the reproductive cycle by daylength and temperature is an important component of the adaptation of plants to their environment. In crop plants it may determine both the overall length of the life cycle and the relative length of the three main phases.

Water or high temperature stress during any of the three developmental phases can affect yield and yield components in

a number of ways. Stress during the vegetative phase reduces leaf area and thus the total photosynthetic potential of the plant. Furthermore, it reduces the amount of assimilates stored in the stem that could be translocated to the grains during grain filling. Stress during GS2 reduces yield by reducing the potential seed number either due to reduced panicle size or due to floret abortion. By shortening the length of GS3, water or high temperature stress could affect grain size and thus yield. This could occur as a result of delay in flowering or a premature cessation of the grain filling process or both. Results of Asana and Williams (1965) and Jenner and Rathjen (1975) indicate temperature rather than water stress stops grain growth prematurely in wheat. In sorghum, elevated temperatures by day or night shortened panicle expansion days and duration of grain filling and reduced grain yield (Eastin, 1976). Downes (1972) reported that day temperatures in the range of 24 to 36 C did not affect sorghum grain yield except at very high night temperatures (31 C). In wheat, Asana and Williams (1965) reported a 16% reduction in yield due to a 6 C rise in day temperature (from 24 to 30 C). Carbon (1973) reported reduced plant growth and tiller numbers in forage sorghum and delayed flowering in grain sorghum due to increased diurnal water stress.

Williams and Shapter (1955) observed that many effects of water stress on ratios of plant parts reflected the fact

increase in yield over controls when passed through an approximately ten-day drought period at early vegetative (6-leaf) stage and rewatered before wilting symptoms developed. Both the total dry matter and grain yield per plant in two maize hybrids were directly related to leaf water potentials at tasselling in plants that were stressed for 0, 3, or 5 days (Soriano and Ginzo, 1975). Water stress during the period of male inflorescence initiation in maize inhibited growth and development of the axillary shoots during the episode of water deficit but promoted it thereafter (Damptey and Aspinall, 1976). As a result, plants subjected to water deficit at that period produced 2 to 3 mature cobs and large axillary shoots at the lower nodes, whereas plants supplied with water throughout produced a single mature cob and relatively small axillary shoots.

The high consumptive water use period for sorghum spans a period of approximately 30 days beginning with mid- to late boot (7 to 10 days before head emergence), lasts through pollination and early grain development and into the milk stage (Jensen and Musick, 1962). This may be one of the reasons for the large decreases in grain yield associated with water stress during this period. Pasternak and Wilson (1969) reported that the degree of emergence of sorghum heads at the beginning of heat treatments determined the amount of damage. High temperatures severely damaged those inflorescences that were in the boot stage and those parts that were

still surrounded by the flag leaf sheaths, but had little effect on parts that had emerged. The greatest reduction in grain sorghum yield occurred when water stress was imposed at the boot stage (Eck and Musick, 1979a; Inuyama, 1978b; Lewis et al., 1974). Yield reductions from stress initiated at early boot resulted from both reduced seed size and seed numbers. Shipley and Regier (1970) reported that heads of grain sorghum hybrid RS 671 failed to emerge when stress occurred at the boot stage. The reductions in yield observed in these studies may be due to temperature rather than a direct effect of water stress. If the temperature of the plant rises above that of the environment the leaf sheaths surrounding the inflorescences act as thermal insulators preventing conductive loss of heat from the plant to the environment (Levitt, 1980). This can cause floret abortion and thus a reduction in seed number. In the study by Eck and Musick (1979a) only seed size was reduced when water stress was imposed at head emergence or later. Inuyama (1980) also reported a reduction in grain yield due to reduced seed size when grain sorghum was subjected to water stress from head emergence through the milk stage.

The biggest effects of water stress on grain yield are usually associated with reductions in seed number. Henckel (1964) reviewed several papers and concluded that the most severe injuries from water stress resulted when water deficits occurred during the sexual cell formation stage. The

reductions in yield at this stage resulted from both a smaller number of kernels and smaller seed size.

Tillering provides an important form of developmental plasticity in some species (eg. wheat). In other species assimilates accumulated prior to seed filling are transferred to the seed during grain growth. Current evidence suggests that when water supply is adequate only a small proportion of the grain dry weight comes from the store of prior assimilates in the stems and roots, but that when stress occurs in the seed filling stage an increased proportion of the prior assimilates is transferred to the head (Gallagher et al., 1976). Soil water stress of -15 bars for eight days during the late vegetative and early grain filling stages in corn reduced number of grains per plant by up to 32%, and the same stress after flowering limited the grain filling process so that yields were reduced by up to 49% (Wilson, 1968a). In the three-week period after silking water deficits reduced maize yields approximately 30% (Claassen and Shaw, 1970). Significant reductions in kernel weights were associated with stress during or after silking. Wilson (1968b) reported that the greatest yields were achieved where plants were well watered after flowering, regardless of the water regime before flowering, with heavier grain compensating for any drop in grain number. Two or more consecutive droughts over the late vegetative and early reproductive phases depressed yields by as much as 66%. Wilson and Allison (1978) reported that mild

drought during grain filling had little effect on final grain yield although it did result in a decrease in total dry matter. Downey (1971) reported a 50% reduction and Krishnamurthy et al. (1975) a 24% reduction in grain yield of maize when water stress occurred during grain filling. In the former case the reduction was attributed to a reduction in seed size while in the latter case it was due to a combination of reduced seed size and seed number. Mirhadi and Kobayashi (1979) reported that water stress at early grain filling reduced panicle weight, number of grains per panicle, and seed size in sorghum. Blum (1973) observed that resistant sorghum hybrids performed better than susceptible ones by producing a relatively higher number of panicles per unit area, and more grains per panicle branch when under stress. Susceptible hybrids performed better than resistant ones under non-stress (irrigated) conditions due to a higher number of panicles per unit area and larger seed size.

Genotypic Differences in Response to Stress

Resistance to stress in crop plants includes both avoidance and tolerance. Stress avoidant plants avoid water or high temperature stress by erecting some barrier to reduce the stress (Levitt, 1980). Such barriers against water stress include a more extensive root system to explore more soil volume; stomatal closure, thicker cuticles, and reduced leaf size to reduce water loss. Barriers against high temperature include transpirational cooling; leaf rolling and changes in

leaf angle to reduce radiation load and thus temperature. Levitt (1980) defined stress tolerance as the ability to undergo without injury a strain that is fatal to a less resistant organism. Sullivan (1971) suggested three criteria that could be used to evaluate drought stress: (a) maintenance of high leaf water potential, (b) stomatal control of diffusive resistance to water loss, and (c) desiccation and heat tolerance. The first two criteria can be classified as avoidance mechanisms as defined earlier. There is considerable variation between and within species in the degree of resistance to water and high temperature stress.

The water potential that six sorghum types were able to withstand, and still recover from, varied from -31 to -48 bars; and the temperature at which 50% injury occurred, as measured by the electrical conductivity method, ranged from 45 to 51.6 C (Sullivan and Eastin, 1974). Significant differences were noted in leaf water potential, leaf diffusive resistance, and water extraction (Blum, 1974b) and the leaf water potential at which an exponential increase in water saturation deficit commenced (Blum, 1974a) among a number of sorghum genotypes grown in the field. Henzell et al. (1975) also observed considerable differences in the stomatal sensitivity to water stress of 23 sorghum genotypes grown in a controlled environment chamber. Nour et al. (1978) found differences in survival rate when they subjected seedlings of ten sorghum cultivars to four successive cycles of water stress. Blum and

Ebercon (1976) also noticed significant differences in recovery rating and post-stress dark respiration of eight sorghum cultivars subjected to water stress. Water stress differentially affected the length of the growth phases of two sorghum cultivars, M35 and NK300 (Stout et al., 1978). Inflorescence development was advanced in M35 and delayed in NK300. The maize hybrid DeKalb 880 outyielded Abati No. 2 when both were subjected to 0, 3, or 5 days of water stress; and grain yield per plant was directly related to leaf water potential at tasselling (Soriano and Ginzo, 1975). Inuyama (1978a) reported that leaf water potential during the stress period was higher in the sorghum hybrid C42y than in E59 when both were subjected to water stress at any stage of growth. Consequently, the former hybrid outyielded the latter under water stress. Krieg (1975) evaluated the genotype-environment stress response as a function of yield and yield components. He found water stress during boot and during bloom to reduce yield in two of the three sorghum genotypes tested. The decreases in yield were attributed to decreases in the number of seeds per head. Parts of heads of RS 671 failed to emerge when stress developed during the boot stage (Shipley and Regier, 1970) but heads of Pioneer 8311 stressed at boot did emerge, although peduncles were shortened (Eck and Musick, 1979a). Regrowth of RS 671 plants stressed at boot caused axillary tillers to develop but not in Pioneer 8311. Axillary tiller growth was also noticed in Pioneer 846 after physio-

logical maturity, when water stress was alleviated by rainfall late in the growing season (Kaigama et al., 1977).

Constable and Hearn (1978) observed varietal differences in the amount of stem reserves transferred to the grains in soybeans subjected to water stress.

Genotypic differences have been observed in the response of some basic physiological processes when plants were subjected to water or high temperature stress. Norcio (1976) reported that the photosynthetic rates of RS 626 declined sharply when temperatures were increased from 40 to 43 C while that of 4104 showed only a minimal decline. At low irradiance the net photosynthetic rate of RS 610 decreased sharply with decrease in relative humidity from 80% to 65% while that of M35-1 remained almost constant (Blum and Sullivan, 1972). At high irradiance net photosynthetic rates in both genotypes declined with decrease in % relative humidity but M35-1 maintained its superiority at all levels of % relative humidity. Sullivan and Eastin (1974) measured oxygen evolution from cell-free extracts of leaves of six sorghum types. The amount of reduction in oxygen evolution when the osmotic potential of the extract was -31 bars from that at -5.4 bars ranged from 91.6% in the 'Milo' type to 57.6% in the 'Hegari' type.

Hybrids are well known for being better buffered against environmental extremes, as compared with their parental lines (McWilliams and Griffing, 1965). An average leaf water potential difference of 6 bars reduced net photosynthetic rates of

sorghum hybrids by 25%, the male parents by 33%, and the female lines by 52% (Krieg, 1977). An 8 to 10-bar difference in leaf water potential during grain filling reduced net photosynthetic rates by 54%, 57%, and 43% for hybrids, males and females, respectively.

In addition to the differences in the inherent ability of species and cultivars to survive periods of water deficit and high temperatures, differences have also been found in their ability to "harden" in response to exposure to periods of water deficit and/or elevated temperatures. Dehydration and overheating of plants modify the colloidal-chemical properties of the protoplasm and metabolism and induce various adaptive responses (Henckel, 1964). Norcio and Sullivan (1976) reported that plants that were pre-heat treated acquired some hardening and were more resistant to thermal inactivation than the controls. Net photosynthesis in some genotypes were reduced due to increased stomatal sensitivity as a result of hardening which increased resistance to CO_2 diffusion. Early, medium and late maturity sorghum hybrids that were pre-heat treated and transplated in the field showed higher heat tolerance and gave higher grain yields, except for the late maturity hybrid that gave a slightly negative yield response (Sullivan et al., 1977).

Drought tolerant plants are generally associated with decreased growth and development, and those that avoid tissue drought most of their life cycle have little ability to

tolerate desiccation under conditions where their avoidance mechanisms are inadequate for keeping the tissues at high water potential (Sullivan, 1972). This argument probably applies equally as well to heat avoidance and heat tolerance.

MATERIALS AND METHODS

EXPERIMENT 1

Water and Temperature Stress Treatments

Two temperature controlled greenhouse bays were used for these experiments. They were set at 30 and 35 C day temperatures and a common night temperature of 20 C. These temperatures were usually maintained, but not always during the course of the study because the cooling facility was inadequate on exceptionally hot summer days and due to lack of heating on unusually cool summer days and nights.

Sorghum was planted in a 1:1:1 mixture of soil, sand, and peat moss in 8-liter plastic pots on June 8, 1979. Pots were arranged in a split plot design with water stress treatments as the main plots and genotypes as subplots with 8 replications in each bay. All plants that were scheduled to be water stressed were subjected to 4 days of preconditioning water stress from 19 days after emergence (DAE) to 22 DAE.

Water stress treatments were 0, 4, 8, and 12 days without irrigation, starting from 35 DAE (8th leaf fully expanded). At 55 DAE (early boot stage) 4 replications of each treatment from the cool bay were transferred to the hot bay and an equal number transferred from the hot to the cool bay. This allowed for 4 replications of each genotype per water stress treatment combination in each of four temperature environments (Cool, 1; Hot--Cool, 2; Hot, 3; and Cool--Hot, 4; Table 1). The plants were then subjected to a second period of 0, 4,

Table 1. Description of environments and genotypes for experiment 1.

Environment	Description	Maximum temperature recorded, °C	
		Emergence to boot	Boot to maturity
1	Cool	34.5	33.0
2	Hot--Cool	43.0	33.0
3	Hot	43.0	40.5
4	Cool--Hot	34.5	40.5

Genotype	Pedigree	SAL Advanced Yield Trial (1978)	
		Yield	Stability to drought
A	WxSC118	High	Stable
B	MxSC33-9-2-2-2	Low	Stable
D	WxOKY16	High	Unstable
E	MxTAM25	High	Unstable

8, and 12 days of water stress starting 58 DAE (late boot to tip-bloom).

Genotypes

The four sorghum hybrids used were developed by Dr. William Ross, USDA, ARS, at the University of Nebraska, Lincoln, They were chosen on the basis of their yield response to various levels of water stress when grown under the line source gradient irrigation system at the University of Nebraska Sandhills Field Laboratory near Tryon, Nebraska in 1978 (Watts et al., 1980). Under the conditions of the Sandhills experiments, the cross of Wheatland x SC118 (A) was high yielding and stable, Martin x SC33-9-2-2-2 (B) was low yielding but stable, the crosses of Wheatland x OKY16 (D) and Martin x TAM25 were both high yielding but unstable (Table 1); where stability denotes the ability of a genotype to produce almost as much grain under severe water stress as under full irrigation (Garrity et al., 1982).

Cultural Practices

Except during the water stress periods plants were kept well watered with either a complete nutrient solution (Table 2) or tap water on alternate days.

Plants were sprayed with Carzol (92% m (((Dimethyl amino) methylene) amino) phenyl methyl carbamate monohydrochloride) at one tablespoon per gallon of water for control of spider mites as needed.

Table 2. Nutrient solution for experiments 1 and 2.

Compound	mg per liter of final solution
KNO_3	600
$Ca(NO_3)_2 \cdot 4H_2O$	950
P_2O_5 (45% Super phosphate)	160
$MgSO_4 \cdot 7H_2O$	490
NH_4NO_3	80*
HEDTA-$Fe(NO_3)_3$	1.0 ml of stock**
H_3BO_3	1.55
$MnSO_4 \cdot H_2O$	.85
$ZnSO_4 \cdot 7H_2O$	.55
$CuSO_4 \cdot 5H_2O$	.13
$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	.15

* Increased by 80 mg for each week of plant growth.

** 9.82 g of HEDTA and 13.02 g of ferric nitrate dissolved in about 200 ml of 1N NaOH and made up to 1 liter with distilled water (See Appendix Table 1 for the complete procedure).

Observations, Measurements and Tests

Temperatures in the two bays were continuously monitored with tempscribes placed about the middle of each bay.

Leaf emergence rates were recorded by noting the date the collars of leaves 3 through 12 became visible. Dates of head emergence, bloom and physiological maturity were also recorded.

Heat and desiccation tolerance tests (Sullivan, 1972) were conducted at various times during the season. Because of the large number of plants involved the tests were spread out so that plants of each water stress treatment were sampled on a different date. Heat and desiccation tolerance tests were conducted at 45 DAE on plants that were water stressed for 4 days; desiccation tolerance tests on genotypes A and E of 8 days water stressed plants at 49 DAE; and heat and desiccation tolerance tests on 12 days water stressed plants at 56 DAE. Heat tolerance tests were conducted on genotypes A and E at 68, 75, and 81 DAE for plants water stressed for 4, 8, and 12 days, respectively. Because of insufficient leaf area for sampling on plants water stressed for 12 days in environments 3 (Hot) and 4 (Cool--Hot) the heat tolerance tests were conducted on plants in environments 1 (Cool) and 2 (Hot--Cool) only. Each time plants in one of the water stress treatments were sampled the control (non-water stressed) plants were also sampled.

Preliminary tests were conducted to determine the

temperature or concentration of polethylene glycol (PEG) 600 that caused about 50% injury to leaf discs as measured with a conductivity bridge. From these preliminary tests a temperature of 53.5 C and 20% solution of PEG 600 in water (v/v) were determined to be adequate.

At harvest plant dry matter was separated into panicles, leaves, stems and tillers. Panicles were further separated into main plant heads, nodal heads and tiller heads. All plant parts were oven dried at 90 C for dry weight determinations. Heads were threshed and grain yield and number of grains determined. Weight of 1000 seeds was determined from a sample of 125 seeds from each panicle (Ross and Kofoid, 1978).

EXPERIMENT 2

This experiment was designed to look at the degree of injury caused by various combinations of heat and desiccation on leaf discs of some sorghum genotypes.

Seeds of three sorghum genotypes, Martin B, Martin x SC33-9-2-2-2 (B in experiment 1) and 226 were started on January 23, 1980. Seeds were arranged along a row about one inch from the edge of a paper towel. The paper towel was rolled and placed in a 600 ml beaker about half-filled with water so that seeds were moistened by capillarity. Three days after germination seedlings were transferred to trays suspended over a dishpan of elongation solution (half-strength concentration of nutrient solution, Table 2). Ten days after germination plants were transferred to 8-liter plastic pots filled with nutrient solution and arranged in randomized complete blocks with six replications. Air was supplied to the roots as described in experiment 3.

Preliminary tests were conducted to determine the concentration of polyethylene glycol (PEG) 600 or temperature that would cause about 50% injury to leaf discs. Tests were also conducted to determine the effect of leaf position and the length of the holding period in the cold room, 18 to 24 hours or 36 to 48 hours (see Table A2).

From the results of the preliminary tests temperatures of 48 and 51 C and concentrations of 15 and 25% PEG in water (v/v) were chosen for further study. It was also noticed

that injury was greater with a longer holding period (36 to 48 hours as compared to 18 to 24 hours) and when the heat treatment was applied to discs without any water added than when they were treated with about 20 ml of water in the tubes. The latter was likely due to the much higher specific heat of water compared to that of air and thus taking longer to heat the leaf discs to injury-causing temperatures.

To make comparisons across treatments more meaningful the heat treatment procedure, as given in Table A2, was slightly modified. Since the treatments that required applying heat while the leaf discs were being desiccated (treatment Nos. 7, 10, 13, and 16, see below) needed to be in the PEG solution during heating, the heat test procedure was modified so that leaf discs were heated in 20 ml of water. Furthermore, the holding period for the heat test was extended to 36 to 48 hours to correspond to that of the desiccation test.

Because of insufficient leaf area in genotype 226, leaf discs were sampled from genotype Martin x SC33-9-2-2-2 at 73 days after germination and from Martin B at 77 days after germination. Because there would not be enough leaf area for all the intended tests even in these genotypes, three blocks were composited into one sample to give two replications for each test on genotype Martin x SC33-9-2-2-2, and the number of tests was reduced for genotype Martin B.

The heat and desiccation treatments applied were:

1. *Heat treatment at 48 C.
2. *Heat treatment at 51 C.
3. *Desiccation with 15% PEG 600[1].
4. *Desiccation with 25% PEG 600[2].
5. Heat treatment at 48 C followed by desiccation with 15% PEG 600.
6. Desiccation with 15% PEG 600 followed by heat treatment at 48 C.
7. Heat treatment at 48 C while being desiccated with 15% PEG 600.
8. *Heat treatment at 48 C followed by desiccation with 25% PEG 600.
9. *Desiccation with 25% PEG 600 followed by heat treatment at 48 C.
10. *Heat treatment at 48 C while being desiccated with 25% PEG 600.
11. *Heat treatment at 51 C followed by desiccation with 15% PEG 600.
12. *Desiccation with 15% PEG 600 followed by heat treatment at 51 C.
13. *Heat treatment at 51 C while being desiccated with 15% PEG 600.

---

[1] 15% PEG 600 = -10 bars (-1.0 MPa)

[2] 25% PEG 600 = -23 bars (-2.3 MPa)

* Only tests conducted on genotype Martin B.

14. Heat treatment at 51 C followed by desiccation with 25% PEG 600.
15. Desiccation with 25% PEG 600 followed by heat treatment at 51 C.
16. Heat treatment at 51 C while being desiccated with 25% PEG 600.

EXPERIMENT 3

Water and Temperature Stress Treatments

Two greenhouse bays were set at the same temperatures as in experiment 1. Sorghum seed was planted in vermiculite on July 7, 1980. Nine days after emergence, on July 18, they were transferred to plastic pots filled with nutrient solution (Table 3). Plants were supplied with a half-strength concentration of this solution until three weeks after emergence (7th leaf fully expanded) and a full concentration of the same solution thereafter.

Pots were arranged in a split plot design with water stress treatments as main plots and genotypes as subplots, with six replications in each bay.

Water stress was imposed by applying 0 (control), 4% (-0.4 MPa) and 7.5% (-0.6 MPa) solution of PEG 600 in water (v/v) to the nutrient solution. The PEG was applied in two increments on two consecutive days to give the final concentrations designated, when plants were in the half-bloom to full-bloom stage. The osmotic stress was removed two weeks later (milk to soft dough stage) by washing plant roots in tap water and completely changing the nutrient solution in the pots. During the treatment period the stress levels were maintained by adjustment of the water levels in the pots. This was done by adding water or water and a measured volume of nutrient solution on alternate days, to each pot.

Table 3. Nutrient solution for experiments 3 to 7.

Compound	mg per liter of final solution
KNO_3	600
$Ca(NO_3)_2 \cdot 4H_2O$	1500
$NH_4H_2PO_4$	20
$MgSO_4 \cdot 7H_2O$	250
NH_4NO_3	300
HEDTA-$Fe(NO_3)_3$	2.0 ml stock**
KCL	3.73
H_3BO_3	1.55
$MnSO_4 \cdot H_2O$	.34
$ZnSO_4 \cdot 7H_2O$	.57
$CuSO_4 \cdot 5H_2O$	.13
H_2MoO_4	.08

** See Table 2, p 27.

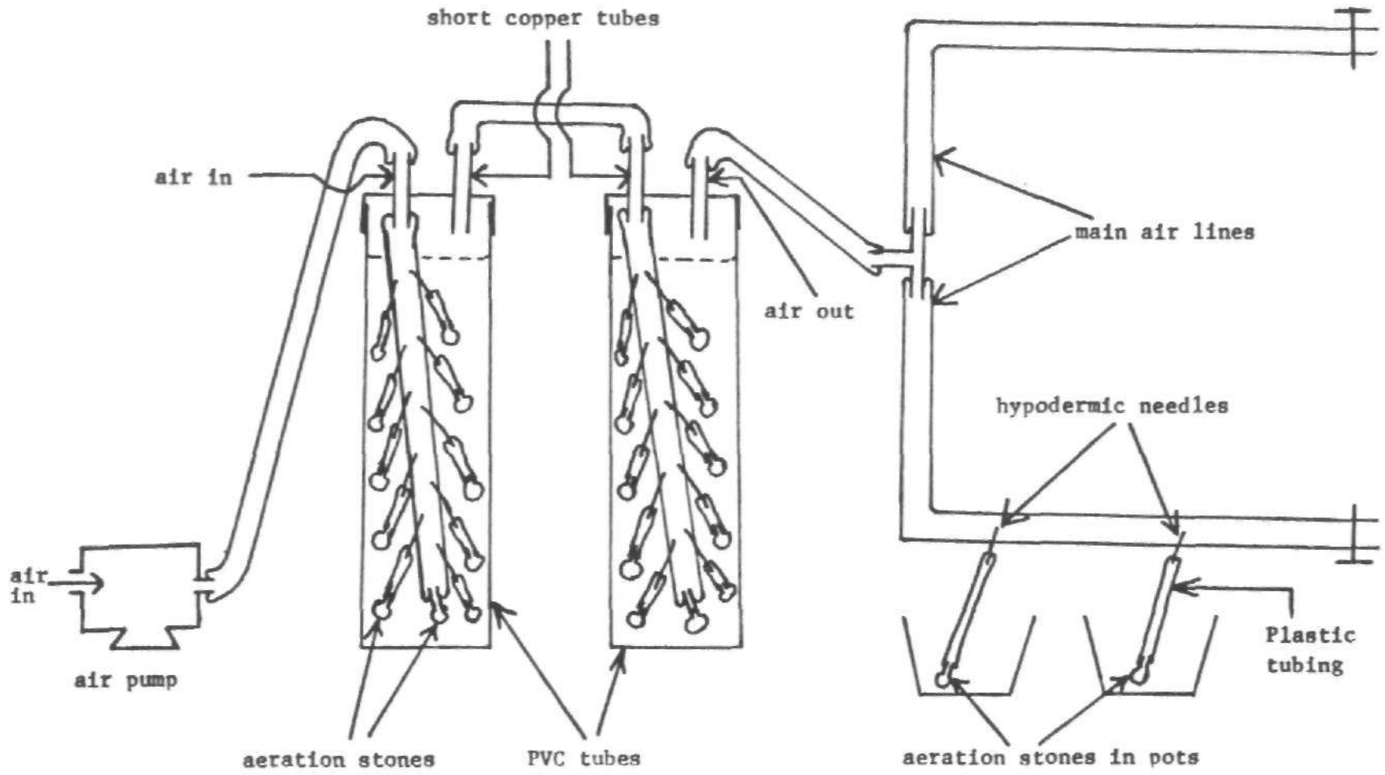
Preparation of Pots for Plant Growth in Nutrient Culture

Ten-liter plastic pots were lined with polyethylene bags and filled with nutrient solution. Pots were covered with 30 cm x 30 cm x 2.5 cm polystyrene foam with 5 cm diameter holes in the middle. The young plants were held in place with foam rubber wrapped around the base of the stem and placed in the holes. Air was continuously supplied to the roots with aeration stones fitted with short pieces of plastic tubing and hypodermic needles which penetrated a main air line coming from an air pump (Fig. 1). The aeration also helped to keep the culture solution well mixed. To reduce evaporation from the pots due to drier air coming from the main line the air was passed through water in two polyvinyl chloride (PVC) tubes (100 cm x 10 cm diameter). Many aeration stones were attached to the main line in the PVC tubes to break up the air bubbles in order to maximize surface contact to well mix the air with the water. The PVC tubes were sealed air-tight with duct tape (Fig. 1). This arrangement supplied moist air to the pots, thus reducing evaporation. The PVC tubes were refilled as needed by siphoning water through the short air outlet copper tubing.

Genotypes

Because of lack of seeds of two of the genotypes used in experiment 1 only two of them, Wheatland x SC118 (A) and Martin x SC33-9-2-2-2-(B) were used in this study. A third hybrid, RS 626 was also included in experiment 3.

Figure 1. Aeration system for plant growth in nutrient culture.



Observations and Measurements

Temperatures in the two bays were continuously monitored with tempscribes placed about the middle of each bay. Relative humidity in the two bays was also recorded periodically with hygrometers placed near the center of the bays.

Leaf emergence rates were recorded by noting the date the collars of leaves 5 through 11 became visible. Dates of head emergence, bloom and physiological maturity (black layer formation) were also recorded.

At harvest plant parts were separated into roots, main plant shoots and tillers. The latter two were further divided into leaves, stems and panicles. All plant parts were oven dried at 90 C for determination of dry weights. Panicles were threshed to determine grain yield and number of grains. The 1000-seed weight was determined from the weight of 125 seeds from each panicle (Ross and Kofoid, 1978).

EXPERIMENT 4

Treatments

Seeds of the three sorghum genotypes used in experiment 3 were planted in germination trays filled with vermiculite. Pots were arranged in randomized complete blocks with 24 replications in each of two greenhouse bays set at 30 and 35 C day temperatures and a common night temperature of 20 C.

Seven days after emergence plants were transferred to pots as described in experiment 3. The root aeration system was also set up as described in experiment 3. In addition to the pots containing plants, 18 blank pots were included in each greenhouse bay. These were pots prepared the same way as the experimental units but had no plants in them and the holes in the polystyrene covers were sealed with duct tape. The blank pots were evenly spaced among the experimental pots in six groups of three in each bay.

Nine liters of nutrient solution (Table 3) were measured into each pot at the beginning of the experiment. The amount of water lost from the blank pots due to the aeration system and free surface evaporation was obtained by measuring the volume of nutrient solution left in the pots at the end of the study.

Measurements

Temperature in the two bays was continuously monitored with tempscribes placed about the middle of each bay.

Plant water use was measured by noting the volume of nutrient solution or water added to each pot during the course of the study. Water use from each pot was estimated by subtracting the volume left in the pot at the end of the study and the loss due to aeration and evaporation, from the total amount added to the pot during the course of the study, as follows:

$$WU = (91 - R_i) + V_i - (91 - R_b)$$

$$= V_i + R_b - R_i$$

Where WU = water use

91 = starting volume (9 liters)

R_i = water remaining in a specific pot i at the end of the study.

V_i = total volume of water added to a specific pot i during the course of the study.

R_b = the average volume of water remaining in 18 blank pots (in each bay) at the end of the study.

Leaf emergence rates were measured by noting the date the collar of each leaf became visible starting from leaf 4 until plants were harvested at the 7th to 10th leaf stage depending on genotype and environment.

Plants were harvested 32 days after emergence and plant parts were separated into roots and shoots. These were oven dried at 90 C for dry weight determinations.

EXPERIMENT 5

Treatments

Sorghum seeds were planted in peat pots filled with vermiculite and arranged in a split plot design with water stress treatments as the main plots and genotypes as the subplots with six replications in each of four temperature environments. The four environments were:

1. Low temperature (LT).
2. High temperature followed by low temperature (HT then LT).
3. High temperature (HT).
4. Low temperature followed by high temperature (LT then HT).

Water stress treatments were 0, -3 bars, and -4.5 bars in the LT and HT environments and -3 bars and -4.5 bars in the two other environments. The ten water stress and temperature treatment combinations thus obtained are given in Table 4.

Application of Treatments

Soon after emergence plants were placed in one of two controlled environmental chambers set at day temperatures of 30 or 40 C and a night temperature of 22 C. Air in the environmental chambers was continuously circulated by drawing air from outside the building with a hose attached to the vacuum side of an air pump. Two hoses attached to the pressure side of the pump were fed into the chambers through holes

Table 4. Description of treatment combinations for experiment 5.

Environment	Water stress(bars)		Description
1	0	(0)+	Low temperature control
1	-3	(-0.3)	Low temperature with low water stress
1	-4.5	(-0.45)	Low temperature with high water stress
2	-3	(-0.3)	High temperature followed by low temperature with low water stress
2	-4.5	(-0.45)	High temperature followed by low temperature with high water stress
3	0	(0)	High temperature control
3	-3	(-0.3)	High temperature with low water stress
3	-4.5	(-0.45)	High temperature with high water stress
4	-3	(-0.3)	Low temperature with low water stress followed by high temperature
4	-4.5	(-0.45)	Low temperature with high water stress followed by high temperature

+ Numbers in parentheses are water stress levels in MPa.

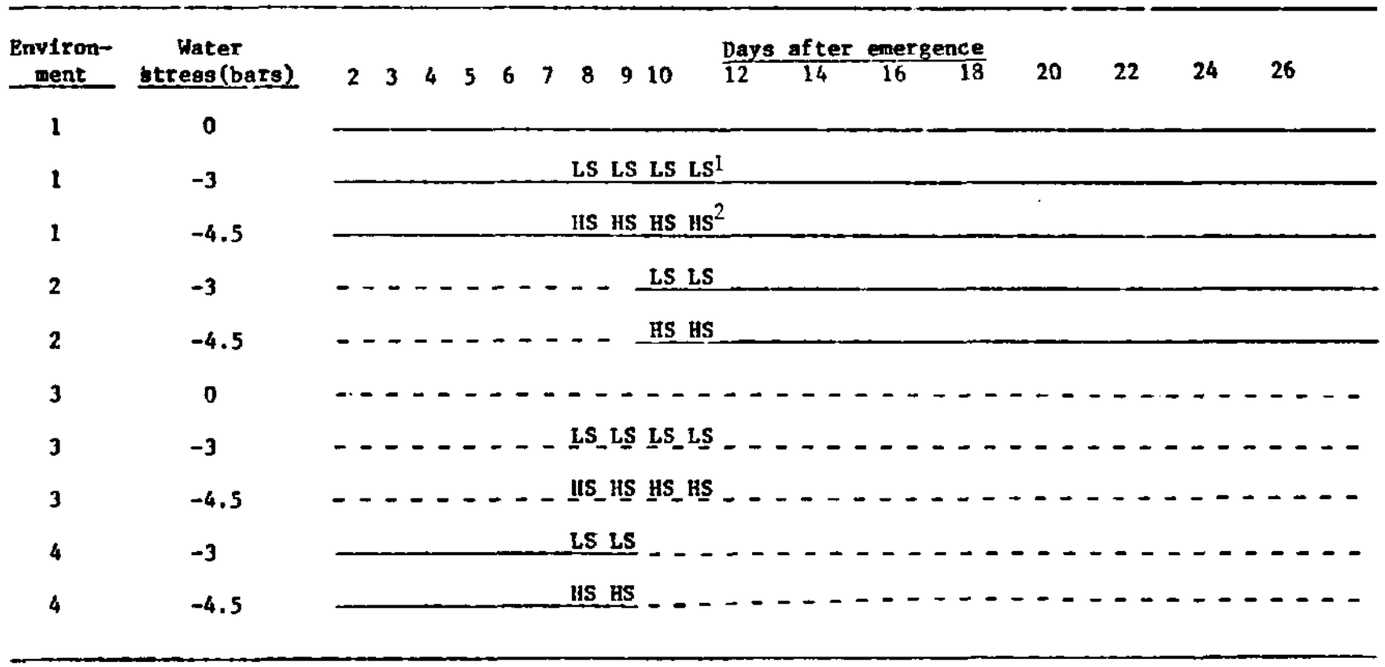
made in the chamber walls. A second air pump was used to continuously draw air out of the chambers.

Eight days after emergence water stress was imposed on all but environment 2 treatments by flooding the pots in 0% (control), 2.5% (low water stress, -3 bars), or 5% (high water stress, -4.5 bars) PEG 600 in dishpans of nutrient solution (Table 3). Two days later PEG was removed from environment 4 treatments and those plants were moved from the 30 C environmental chamber to the 40 C environmental chamber. At the same time environment 2 treatments were moved from the 40 C environmental chamber to the 30 C environmental chamber and then water stressed by flooding with 2.5% or 5% PEG 600. Water was added to the dishpans two times daily during the stress period so as to maintain the nutrient solution levels and thus the stress levels desired. Another two days later at 12 days after emergence, water stress was removed from all the treatments (Fig. 2) by washing off the PEG from the roots by several flushings with tap water and a final flushing with nutrient solution. Plants were transferred to trays and kept watered with nutrient solution (Table 3) or tap water on alternate days.

Genotypes

Two of the sorghum genotypes used were selections from sorghum population NP9BR (Ross, 1974). Genotype 121 was a high yielding water stress-tolerant line and 160 was a low

Figure 2. Summary of temperature and water stress treatments for experiment 5.



yielding line susceptible to water stress in Nebraska Sandhills Field Laboratory experiments (Garrity et al., 1982; Watts et al., 1980). The third genotype was used as a check, hybrid RS 626.

Measurements

Light, temperature and relative humidity in the controlled environmental chambers were continuously monitored with a LICOR[1] LI 190S quantum sensor and a Campbell Scientific[2] 201 relative humidity/temperature probe respectively, attached to a Campbell Scientific CR 21 micrologger. Lights were kept on for 10 hours daily from 0700 to 1700 hours central standard time (CST) while day temperatures were maintained for 14 hours from 0600 to 2000 hours CST.

Net carbon exchange was determined with the use of a portable plexiglass chamber (Sullivan et al., 1976) at 18 and 24 days after emergence and changes in CO_2 concentration analyzed with an infrared gas analyzer by the technique of Clegg et al. (1978).

Leaf expansion was evaluated by measuring the maximum leaf length and maximum width (Bishnoi, 1966; McCree and Davies, 1974; Stickler et al., 1961) of leaves 5 and 6.

A regression line of leaf area on the product of length x width was previously determined for each genotype. The

---

[1] LICOR Inc., Lincoln, Nebraska.

[2] Campbell Scientific Inc., Logan, Utah.

dimensions of leaves 2 through 18 for genotypes 121 and RS 626 and leaves 2 through 12 for genotype 160 were measured in three replications and this was related to their actual area as measured with a LICOR LI 3100 leaf area meter. These regression lines were used to estimate the actual area of the leaves measured in the study.

At 19 days after emergence three replications of each treatment were harvested and oven dried at 90 C for dry weight determination. The other three replications were harvested 27 days after emergence and their dry weights also determined. Rates of dry matter accumulation were estimated from the differences in weights between the two harvests.

EXPERIMENT 6

Treatments

The treatment combinations were the same as in experiment 5 with a few slight changes. The high temperature was slightly reduced to 38 C because 40 C was found to cause leaf scorching even in control (non-water stressed) plants. Controls were included in environments 2 and 4 to give a total of 12 treatment combinations (Table 5).

The length of time plants were flooded with PEG 600 was also modified so that all PEG treatments were applied for two days only (compare Figs. 2 and 3).

The same three genotypes RS 626, 121 and 160 and the same experiemental design as used in experiment 5 were used.

Measurements

Light levels, temperature and relative humidity in the two controlled environmental chambers were continuously monitored as described in experiment 5.

Leaf expansion was evaluated by measuring the maximum leaf length and maximum width starting from leaf three until plants were harvested at the 7th or 8th leaf stages depending on genotype, Leaf area was determined by substituting the product of length x width in regression equations developed for each genotype in experiment 5.

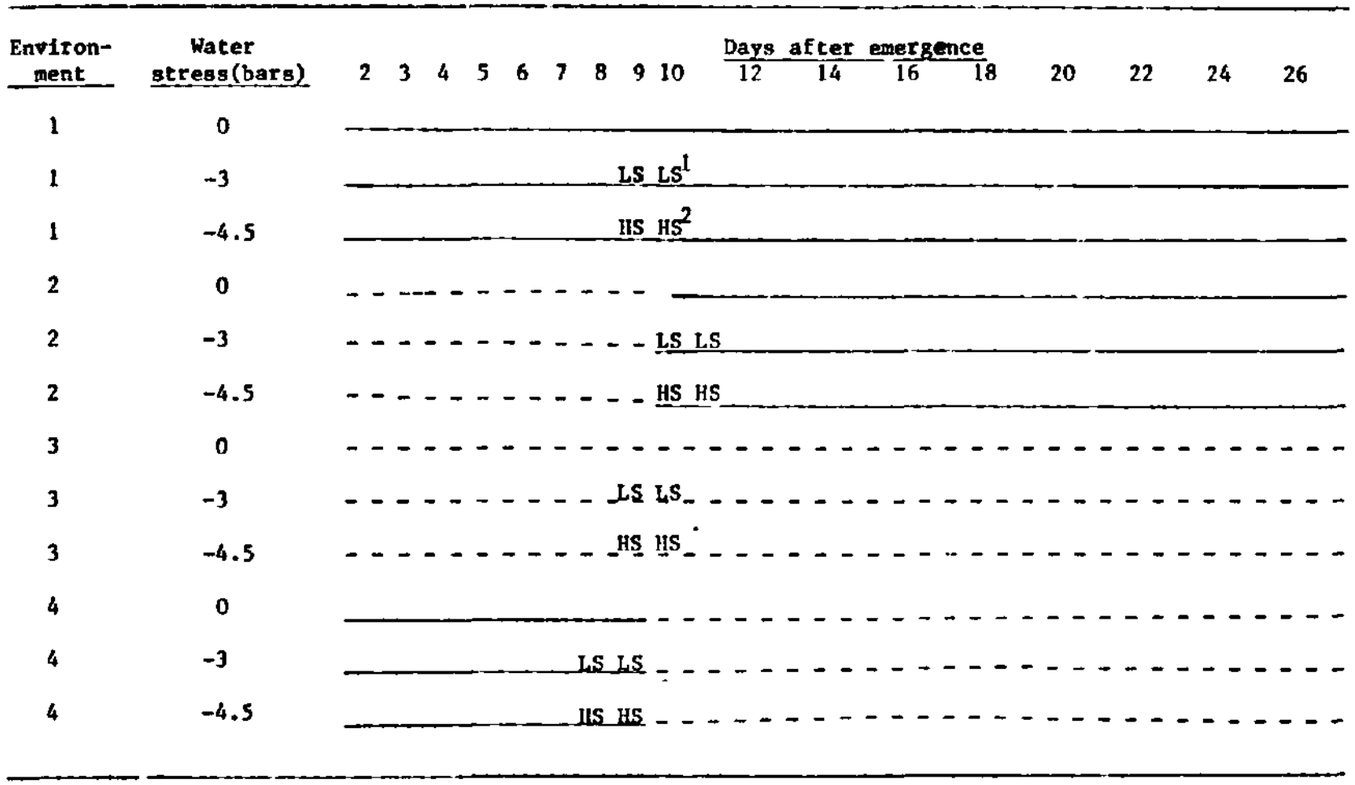
Net carbon exchange was measured with the use of a portable plexiglass chamber (Sullivan et al., 1976) at 18 and

Table 5. Description of treatment combinations for experiment 6.

Environment	Water stress(bars)		Description
1	0	(0)+	Low temperature control
1	-3	(-0.3)	Low temperature with low water stress
1	-4.5	(-0.45)	Low temperature with high water stress
2	0	(0)	High temperature followed by low temperature
2	-3	(-0.3)	High temperature followed by low temperature with low water stress
2	-4.5	(-0.45)	High temperature followed by low temperature with high water stress
3	0	(0)	High temperature control
3	-3	(-0.3)	High temperature with low water stress
3	-4.5	(-0.45)	High temperature with high water stress
4	0	(0))	Low temperature followed by high temperature
4	-3	(-0.3)	Low temperature with low water stress followed by high temperature
4	-4.5	(-0.45)	Low temperature with high water stress followed by high temperature

+ Numbers in parentheses are water stress levels in MPa.

Figure 3. Summary of temperature and water stress treatments for experiment 6.



[1] LS = low water stress
[2] HS = high water stress

25 days after emergence and changes in CO_2 concentration analyzed with an infrared gas analyzer by the technique of Clegg et al. (1978).

The levels of CO_2 in the two chambers were monitored between 18 and 25 days after emergence. Five sub-samples of air going into and out of each environmental chamber were drawn with syringes at each sampling period. The CO_2 content was analyzed by the technique of Clegg et al. (1978).

Three replications of each treatment were harvested at 19 days after emergence and the other three replications at 26 days after emergence. Dry weights at both harvests were determined by oven drying at 90 C. Rates of dry matter accumulation were estimated from the differences in weights between the two harvests.

EXPERIMENT 7

Treatments

The treatment combinations were the same as in experiment 5 with a few variations in the method of application.

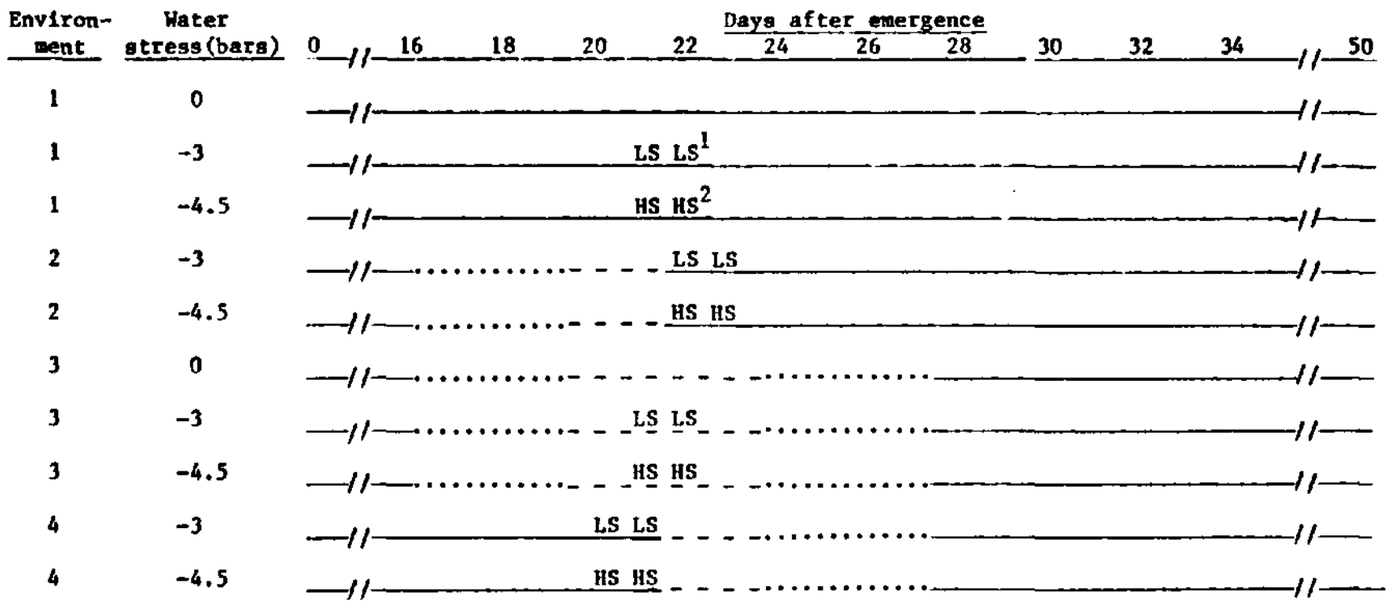
Both controlled environmental chambers were started out at the same day temperature (30 C) and this was maintained for the duration of the study in the low temperature environmental chamber. In the other chamber the day temperature was raised to 35 C at 17 days after emergence and to 37 C at 20 days after emergence. After the water stress was relieved the temperature was again lowered to 35 C at 24 days after emergence and to 30 C at 28 days after emergence (Fig. 4).

The same genotypes used in experiments 5 and 6 were used in this study. Pots were arranged in a split plot design with water stress treatments as main plots and genotypes as subplots with 5 replications in each of the four temperature environments.

Measurements

Light, temperature and relative humidity were again continuously monitored with sensor signals recorded with a Campbell Scientific CR 21 micrologger. Lights were on for 12 hours daily from 0600 to 1800 hours central standard time (CST) and day temperatures were maintained for 14 hours from 0600 to 2000 hours CST.

Figure 4. Summary of temperature and water stress treatments for experiment 7.



30 C

35 C

37C

[1] LS = Low water stress
[2] HS = high water stress

Leaf expansion was evaluated by measuring the maximum length and maximum width of each leaf from leaf 2 until plants were harvested at the 11th to 13th leaf stages depending on genotype and treatment. Leaf area was determined by substituting the product of leaf length x width in the regression equations developed for each genotype in experiment 5.

Plants were harvested 50 days after emergence and oven dried at 90 C for dry weight determinations.

RESULTS AND DISCUSSION

EXPERIMENT 1

Leaf Emergence Rate

Leaf development was completed between 50 and 55 days after emergence. Leaf emergence rates were slightly faster for plants that completed their vegetative growth in the cool environment (environments 1 and 4) than for those in the hot environment (environments 2 and 3). In all genotypes collars of comparable leaves became visible a day or two earlier in the cool environment than they did in the hot environment for the control (non-water stressed) and mildly water stressed (4 days) plants. Downes (1968) found leaf appearance rate in grain sorghum to increase linearly with weighted average daily temperatures between 13 and 23 C. The weighted average temperature during the period of leaf development in this study was near the 23 C mark in the cool environment and about 26 C in the hot environment (Table 6). Tollenaar et al. (1979) also observed leaf appearance rate in corn to increase with day temperatures between 10 and 30 C but noticed a decline when day temperature increased to 35 C.

When the water stress period increased to 8 or 12 days the difference in the rates of leaf emergence between the two environments increased to 3 to 5 days. There were no differences in leaf emergence rates between control and mildly water stressed plants in either environment, but leaf emergence rates decreased with increased water stress to 8 and 12 days in both environments.

Table 6. Ten-day averages of minimum, maximum, and weighted average temperatures (C) for the four environments in experiment 1.

Days after emergence	Environment											
	1 (Cool)			2 (Hot--Cool)			3 (Hot)			4 (Cool--Hot)		
	Mean min.	Mean max.	Average	Mean min.	Mean max.	Average	Mean min.	Mean max.	Average	Mean min.	Mean max.	Average
	Temperature (C)											
0-10	17.4	31.3	23.0	16.2	38.0	25.3	16.2	38.0	25.3	17.4	31.3	23.0
11-20	17.1	32.1	23.0	16.5	39.5	25.7	16.5	39.5	25.7	17.1	32.1	23.0
21-30	17.7	29.3	21.4	17.0	39.9	23.2	17.0	33.9	23.2	17.7	29.3	21.4
31-40	17.3	31.9	23.5	16.3	39.8	26.5	16.3	39.8	26.5	17.3	31.9	23.5
41-50	18.7	30.5	23.2	18.3	40.5	27.7	18.3	40.5	27.7	18.7	30.5	23.2
51-60	18.2	30.6	22.9	18.0	36.3	25.5	18.0	39.6	27.4	18.2	33.9	24.8
61-70	16.2	26.3	19.7	16.2	26.3	19.7	15.7	34.7	24.0	15.7	34.7	24.0
71-80	16.5	28.4	20.8	16.5	28.4	20.8	16.7	38.0	25.2	16.7	38.0	25.2
81-90	17.3	30.1	22.2	17.3	30.1	22.2	17.5	38.2	26.4	17.5	38.2	26.4
91-100	12.0	27.6	18.5	12.0	27.6	18.5	12.7	36.8	23.0	12.7	36.8	23.0
101-110	11.1	28.3	18.5	11.1	28.3	18.5	11.5	38.3	23.0	11.5	38.3	23.0

In addition to decreasing the rate of leaf emergence visual observations indicated that 8 and 12 days of water stress reduced leaf size. Leaves tended to be shorter and narrower in these treatments. Acevedo et al. (1971) also observed that reduced growth of maize leaves during a short and mild water stress was completely offset by a rapid transitory phase of growth following release of stress so that there was no net reduction in total elongation, but it was not enough to offset the reduction in growth when water stress was more severe. In contrast, elevated temperatures were found to increase leaf size. Measurements of leaf lengths and leaf widths of leaves 5 and 8 were made on 16 plants of each genotype in each environment before plants were subjected to water stress. In all four genotypes leaves were longer and in general, slightly wider in the hot environment than they were in the cool environment (Table 7).

In control and mildly water stressed plants leaf emergence rates were similar for genotypes A, D and E but genotype B exerted its leaves 2 to 3 days later. When the water stress period increased to 8 and 12 days genotype B caught up with the other genotypes and they all exerted comparable leaves at about the same time.

Reproductive Development

In non-water stressed plants there was no consistent trend in the number of days to bloom for the various environments. Exposure to high temperatures during the vegetative

Table 7. Lengths and widths (cm) and length x width (cm^2) of leaves 5 and 8 measured before water stress was imposed on four sorghum hybrids grown under two temperature environments.

Node	Genotype	Cool Environment Leaf Length	Cool Environment Leaf Width	Cool Environment L x W	Hot Environment Leaf Length	Hot Environment Leaf Width	Hot Environment L x W
5	A	33.1a[1]	2.46a	81.3a	35.2a	2.55a	90.2a
	B	31.1b	2.44a	76.1ab	32.1c	2.51a	81.2b
	D	31.0b	2.25b	70.7b	33.9b	2.33b	79.0b
	E	31.4ab	2.24b	70.8b	32.9bc	2.19c	72.9c
8	A	61.9ab	4.00bc	248b	63.8a	4.11ab	262a
	B	63.4a	4.29a	272a	63.8a	3.96ab	253ab
	D	58.6c	3.78c	222c	61.3b	3.94b	242b
	E	60.2bc	4.21ab	254ab	62.1ab	4.15a	258a

Overall Means

Environment	Leaf 5 Length	Leaf 5 Width	Leaf 5 L x W	Leaf 8 Length	Leaf 8 Width	Leaf 8 L x W
Cool	31.7b	2.35a	74.7b	61.0b	4.07a	249a
Hot	33.5a	2.40a	80.8a	62.8a	4.04a	254a
Genotype						
A	34.2a	2.51a	85.8a	62.8a	4.06a	255a
B	31.7b	2.48a	78.6b	63.6a	4.13a	263a
D	32.4b	2.30b	7.49bc	60.0b	3.86b	232b
E	32.3b	2.22b	71.8c	61.2b	4.18a	256a

[1] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test.

and early reproductive phases of growth (environments 2 and 3) tended to delay bloom when it was coupled with water stress (Table 8). This is in contrast to the results of Pasternak and Wilson (1969) where they reported that high temperatures accelerated anthesis by about four days. In their study however, high day temperatures (42 C) were coupled with fairly high (32 C) night temperatures as well.

In environments 1, 2 and 4 mild water stress hastened bloom by up to 3 days depending on genotype and environment (Table 8), but bloom was delayed by moderate (8 days) and severe (12 days) water stress. Carbon (1973) also reported delayed flowering in grain sorghum due to increased diurnal water stress. In environment 3 where plants were exposed to elevated temperatures throughout their growth, even mild water stress delayed flowering. Under severe water stress only genotype A in environments 1 and 4 and genotype D in environments 1, 2 and 4 continued their growth to reach bloom (Table 8). All other plants either died from the severe stress or continued growth only vegetatively by producing new tillers.

In all the environments genotype D reached bloom 1 to 3 days earlier than genotypes A and E, and genotype B reached bloom 3 to 5 days later than genotypes A and E.

Under well watered (control) and mildly water stressed (4 days) conditions plants that were exposed to high temperatures during the latter half of their growth (environments

Table 8. Days from emergence to half-bloom and to physiological maturity for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Days to Half-bloom, Genotype A	B	D	E	Days to Physiological maturity, Genotype A	B	D	E
		Number of Days							
1 (Cool)	0	60	65	59	60	88	95	92	92
	4	59	66	58	60	88	95	91	92
	8	62	68	63	63	91	97	93	93
	12	66	--	65	--	95	--	104	--
2 (Hot--Cool)	0	62	67	59	62	88	95	92	92
	4	60	65	59	62	88	95	91	92
	8	65	--	64	65	91	--	93	95
	12	--	--	68	--	--	--	104	--
3 (Hot)	0	61	67	59	61	85	92	89	89
	4	62	68	60	62	85	92	89	89
	8	66	--	63	66	--	--	93	94
	12	--	--	--	--	--	--	--	--
4 (Cool--Hot)	0	63	66	60	63	85	92	89	89
	4	60	64	59	63	85	92	89	89
	8	63	--	60	63	--	--	96	--
	12	66	--	64	--	--	--	96	--

3 and 4) reached physiological maturity about 3 days earlier than those that remained in the cool environment throughout (environment 1) or those that were transferred from the hot to the cool environment at the boot stage of growth (environment 2). Thus high temperatures during bloom and grain filling stages of growth shortened the number of grain filling days. This supports the finding by Eastin (1976) that elevated temperatures by day or night shortened the duration of grain filling.

Within the individual environments 4 days of water stress had no effect on the number of days taken to reach physiological maturity (Table 8). Eight days of water stress delayed physiological maturity by 1 to 3 days, and in those plants that continued their growth 12 days of water stress delayed physiological maturity by 7 to 12 days. This latter case was more likely due to near cessation of growth during the stress period and continued growth after the stress was relieved. These findings suggest that elevated temperatures rather than water stress caused cessation of grain growth in sorghum. This is in line with the findings of Asana and Williams (1965) and Jenner and Rathjen (1975) in wheat.

Tillering

There were marked differences in tillering habit of plants between environments, between water stress treatments within environments, and between genotypes within water stress treatments.

Table 9. Average tiller wieght (g per plant) for four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E
		Weight of Tillers			
1 (Cool)	0	---	---	---	---
	4	---	---	---	---
	8	---	---	---	---
	12	6.1 (4)[1]	2.7 (7)	---	8.8 (4)
2 (Hot--Cool)	0	---	---	---	---
	4	---	---	---	---
	8	---	---	---	4.7 (5)
	12	5.7 (7)	4.9 (4)	---	6.2 (6)
3 (Hot)	0	---	---	---	---
	4	---	2.4 (2)	---	1.2 (1)
	8	8.9 (5)	3.4 (6)	7.9 (4)	10.1 (6)
	12	7.7 (5)	8.3 (6)	4.2 (2)	19.4 (8)
4 (Cool--Hot)	0	1.0 (1)	---	---	---
	4	1.6 (1)	1.8 (1)	---	3.1 (3)
	8	6.6 (3)	2.5 (4)	5.4 (1)	7.8 (3)
	12	6.0 (8)	5.1 (6)	7.5 (2)	9.1 (7)

[1] Numbers in parentheses are the number of plants in the mean

Plants that remained in the cool environment throughout their growth (environment 1) and those that were transferred from the hot to the cool environment at the boot stage (environment 2) did not produce any tillers except under severe (12 days) water stress (Table 9). Genotype D did not tiller in environments 1 and 2 even under severe water stress. In environment 2 genotype E tillered even under moderate (8 days) water stress. In plants that were exposed to high temperatures after the boot stage (environments 3 and 4) all genotypes tillered when subjected to 8 or 12 days of water stress (Table 9). In environment 4 a few plants of genotypes A, B and E tillered even under mild (4 days) water stress. Pasternak and Wilson (1969) also observed that heat treatments at head emergence resulted in development of tillers from both basal and upper nodes.

Plant Height

Plant height at maturity is presented in Tables 10 and 10a and plotted against days of water stress in Figure 5. Plant height was severely affected by water stress especially when coupled with elevated temperatures during the vegetative phase of growth. All four genotypes responded differently to water stress and to temperature treatments. Except in genotype B 4 days of water stress had little effect on plant height in any of the environments.

Plant height in genotype A was only slightly reduced by

Table 10. Plant height (cm) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Plant Height				
1 (Cool)	0	128ab[1]	143a	97d	111cd	120a[2]
	4	118bc	143a	109cd	108cd	119a
	8	121bc	107cd	110cd	105d	111a
	12	107cd	63e	98d	76e	86b
	mean	119a[3]	114a	104b	100b	
2 (Hot--Cool)	0	119bc	136a	115bc	114c	121a
	4	130ab	121bc	118bc	116bc	121a
	8	108c	78e	110c	94d	98b
	12	63f	62f	75ef	64f	66c
	mean	105a	100ab	105a	97b	
3 (Hot)	0	118a	119a	112ab	111ab	115a
	4	119a	112ab	111ab	113ab	114a
	8	98bcd	85de	103abc	92cde	94b
	12	84de	50f	76e	54f	66c
	mean	105a	91b	101a	92b	
4 (Cool--Hot)	0	118abcd	131a	96efgh	107cde	113a
	4	126ab	119abc	107cde	106cdef	115a
	8	115bcd	86hi	107cde	104defg	103b
	12	92gh	65j	92gh	77ij	81c
	mean	113a	100b	101b	98b	

Overall Means

Environment	Plant height	Water stress	Plant height	Genotype	Plant height
1	109a[2]	0	117a	A	110a
2	101ab	4	117a	B	101b
3	97b	8	102b	D	102b
4	103ab	12	75c	E	97c

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

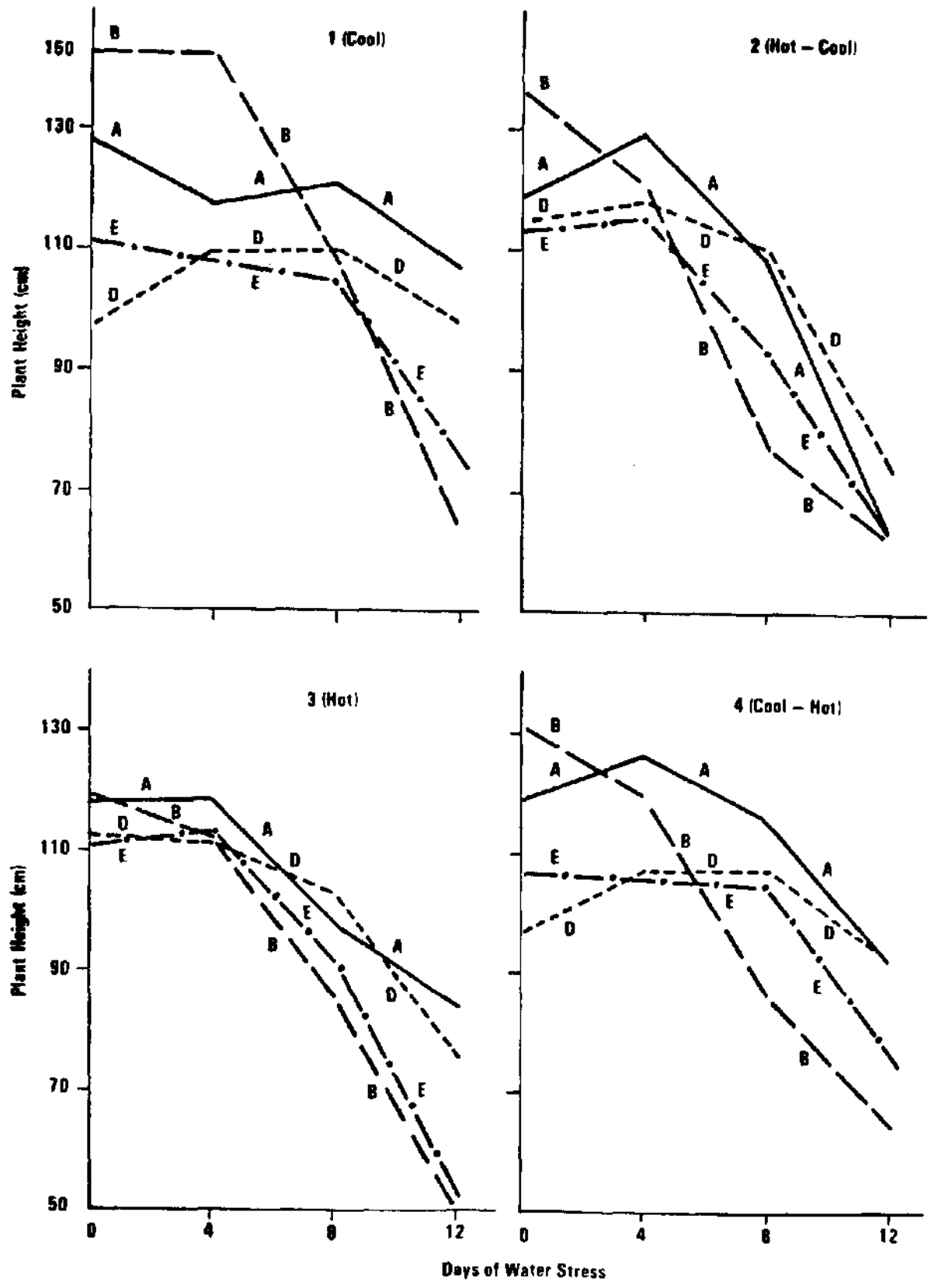
Table 10a. Plant height expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	111	76	87	93
	4	92	111	85	84	93
	8	94	84	86	81	86
	12	83	49	76	59	67
	mean	92	89	81	78	
2 (Hot--Cool)	0	93	106	89	88	94
	4	101	94	92	90	94
	8	84	61	86	73	76
	12	49	49	58	49	51
	mean	82	78	81	75	
3 (Hot)	0	92	93	87	86	90
	4	92	87	87	88	89
	8	76	66	80	71	74
	12	65	39	59	42	51
	mean	81	71	78	72	
4 (Cool--Hot)	0	92	102	75	83	88
	4	98	93	83	82	89
	8	90	67	83	81	80
	12	71	51	72	60	63
	mean	88	78	78	77	

Overall Means

Environment	Plant height(%)	Water stress	Plant height(%)	Genotype	Plant height(%)
1	85	0	91	A	85
2	79	4	91	B	79
3	75	8	79	D	80
4	80	12	57	E	75

Figure 5. Plant height (cm) of 4 sorghum hybrids plotted against days of water stress by environments.



8 days of water stress in environments 1 and 4 but 12 days of water stress reduced plant height by 17 and 23% respectively. Height was reduced by 10 and 47% in environment 2 and by 17 and 29% in environment 3 by 8 and 12 days of water stress, respectively (Tables 10 and 10a).

Plant height in genotype B was the most severely affected by both water stress and by temperature. In environment 1 it was not affected by 4 days of water stress but was reduced by 25% and 56% respectively, by 8 and 12 days of water stress. Plant height was reduced by 11, 43, and 56% in environment 2; by 6, 29, and 58% in environment 3; and by 9, 34 and 50% in environment 4, by 4, 8 and 12 days of water stress, respectively (Tables 10 and 10a).

As in genotype A plant height in genotype E was only slightly reduced by 8 days of water stress in environments 1 and 4, but 12 days of water stress reduced plant height by 32 and 28%, respectively. Height was reduced by 18 and 44% in environment 2 and by 17 and 51% in environment 3 by 8 and 12 days of water stress, respectively (Tables 10 and 10a).

Yield and Yield Components

Panicle Size

Weight of panicles is presented in Tables 11 and 11a and plotted against days of water stress in Figure 6. Except under severe (12 days) water stress panicle weight was greatest in environment 2. When water stress was severe

Table 11. Panicle weight (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Panicle Weight				
1 (Cool)	0	21.1cde[1]	43.0a	14.8def	33.7b	28.2a[2]
	4	16.8cdef	40.1ab	19.0cde	25.1c	25.3a
	8	16.9cdef	23.3cd	16.2def	19.7cde	19.0b
	12	9.5fg	5.7g	13.8efg	8.9fg	9.5c
	mean	16.1c[3]	28.0a	16.0c	21.9b	
2 (Hot--Cool)	0	29.1de	48.8a	30.9cde	37.6bc	36.6a
	4	27.0ef	45.1ab	28.8de	36.5cd	34.4a
	8	20.3fg	17.4g	24.2efg	16.2gh	19.5b
	12	4.0i	3.2i	9.3hi	5.5i	5.5c
	mean	20.1b	28.6a	23.3b	24.0b	
3 (Hot)	0	26.3c	42.5a	24.2c	33.6b	31.6a
	4	27.6bc	25.9c	28.4bc	28.9bc	27.7a
	8	9.3de	22.1c	13.1d	10.3de	13.7b
	12	2.4f	1.0f	2.3f	4.5ef	2.6c
	mean	16.4b	22.9a	17.0b	19.3b	
4 (Cool--Hot)	0	17.1d	40.0a	20.4cd	28.3b	26.5a
	4	17.5d	29.3b	20.0cd	24.3bc	22.8ab
	8	15.0d	20.7cd	15.5d	17.1d	17.1b
	12	3.0e	4.5e	8.3e	3.3e	4.8c
	mean	13.2c	23.6a	16.1b	18.3b	

Overall Means

Environment	Panicle weight	Water stress	Panicle weight	Genotype	Panicle weight
1	20.5ab[2]	0	30.7a	A	16.5c
2	24.0a	4	27.6b	B	25.8a
3	18.9ab	8	17.3c	D	18.1c
4	17.8b	12	5.6d	E	20.9b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

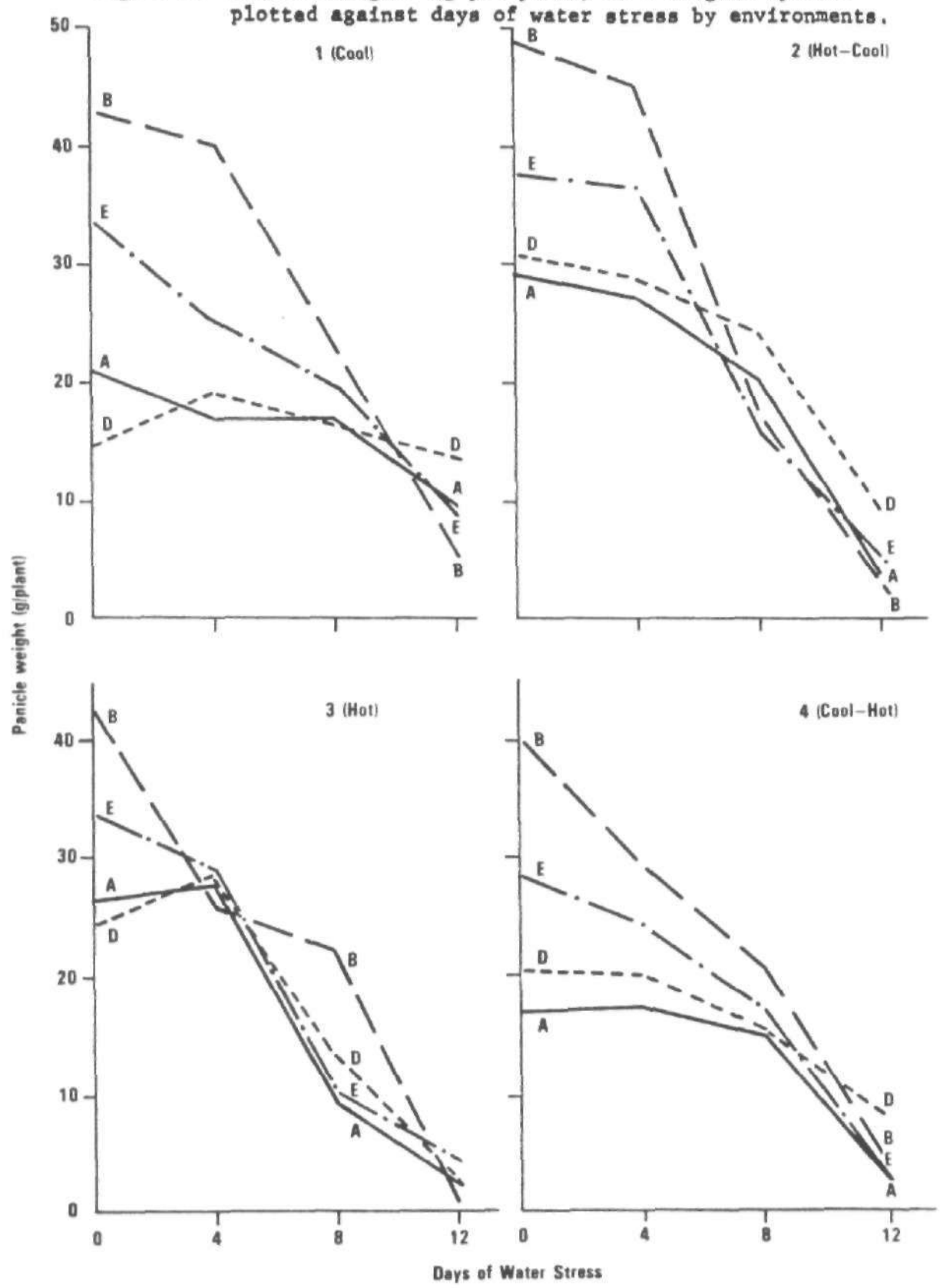
Table 11a. Panicle weight per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	204	70	160	134
	4	80	190	90	119	120
	8	80	110	77	93	90
	12	45	27	65	42	45
	mean	76	133	76	104	
2 (Hot--Cool)	0	138	231	146	178	173
	4	128	214	136	173	163
	8	96	82	115	77	92
	12	19	15	44	26	26
	mean	95	136	110	114	
3 (Hot)	0	125	201	115	159	150
	4	131	123	135	137	131
	8	44	105	62	49	65
	12	11	5	11	21	12
	mean	78	109	81	91	
4 (Cool--Hot)	0	81	190	97	134	126
	4	83	139	95	115	108
	8	71	98	74	81	81
	12	14	21	39	16	23
	mean	63	112	76	87	

Overall Means

Environment	Panicle weight(%)	Water stress	Panicle weight(%)	Genotype	Panicle weight(%)
1	97	0	146	A	78
2	114	4	130	B	122
3	90	8	82	D	86
4	84	12	27	E	99

Figure 6. Panicle weight (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments.



panicle weights were greatest in environment 1. Under control (well watered) and mild water stress (4 days) panicle weights were greater in environment 3 than in environments 1 and 4 but when water stress became moderate or severe panicle weights were greater in the latter two environments. Exposure to high temperatures during panicle initiation and expansion (environments 2 and 3) may have caused more rapid growth and thus, larger panicles. The lower panicle weights in environment 3 especially under moderate and severe water stress was likely due to exposure to high temperatures during seed set.

In general panicle weights decreased with water stress in all environments and for all four genotypes. The differences between control (non-water stressed) and mild (4 days) water stress were however not significant in any of the environments (Tables 11 and 11a).

Except under severe water stress genotype B in general had the highest panicle weight in all environments. It was followed by genotype E and genotypes A and D had the lowest panicle weights. When water stress was severe genotype B had the lowest panicle weight (Tables 11 and 11a, and Fig. 6).

Seed Numbers

Seed numbers are presented in Tables 12 and 12a and plotted against days of water stress in Figure 7. With the single exception of genotype D in environment 1 number of seeds per panicle generally decreased with water stress for

Table 12. Number of seeds per plant for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Number of Seeds				
1 (Cool)	0	842bc[1]	1115a	582de	985ab	881a[2]
	4	731cd	977ab	675cde	820bc	801a
	8	530de	522de	710cde	479e	560b
	12	226f	244f	478e	166f	278c
	mean	582b[3]	714a	611ab	612ab	
2 (Hot--Cool)	0	885bc	1309a	872bc	1035b	1025a
	4	974bc	1049b	789cd	874bc	921a
	8	584e	539e	624de	258f	501b
	12	115f	64f	210f	100f	122c
	mean	639b	740a	624b	567b	
3 (Hot)	0	1132a	1128a	856abc	1034ab	1038a
	4	894abc	669cd	889abc	846bc	825b
	8	142a	643cd	421d	135e	334c
	12	57e	31e	7e	17e	29d
	mean	556a	618a	542a	509a	
4 (Cool--Hot)	0	725bcde	1228a	750bcd	915b	905a
	4	780bcd	658cdef	678cdef	855bc	743a
	8	474fg	594def	504ef	478fg	512b
	12	9i	168hi	279gh	0i	114c
	mean	497b	662a	553b	562ab	

Overall Means

Environment	Seed number	Water stress	Seed number	Genotype	Seed number
1	630a[2]	0	962a	A	569b
2	642a	4	822b	B	683a
3	556a	8	477c	D	582b
4	569a	12	136d	E	563b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 12a. Number of seeds per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	132	69	117	105
	4	87	116	80	97	95
	8	63	62	84	57	67
	12	27	29	67	20	33
	mean	69	85	73	73	
2 (Hot--Cool)	0	105	155	104	123	122
	4	116	125	94	104	109
	8	69	64	74	31	60
	12	14	8	25	12	14
	mean	76	88	74	67	
3 (Hot)	0	134	134	102	123	123
	4	106	79	106	100	98
	8	17	76	50	16	40
	12	7	4	1	2	3
	mean	66	73	64	60	
4 (Cool--Hot)	0	86	146	89	109	107
	4	93	78	81	102	88
	8	56	71	60	57	61
	12	1	20	33	0	14
	mean	59	79	66	67	

Overall Means

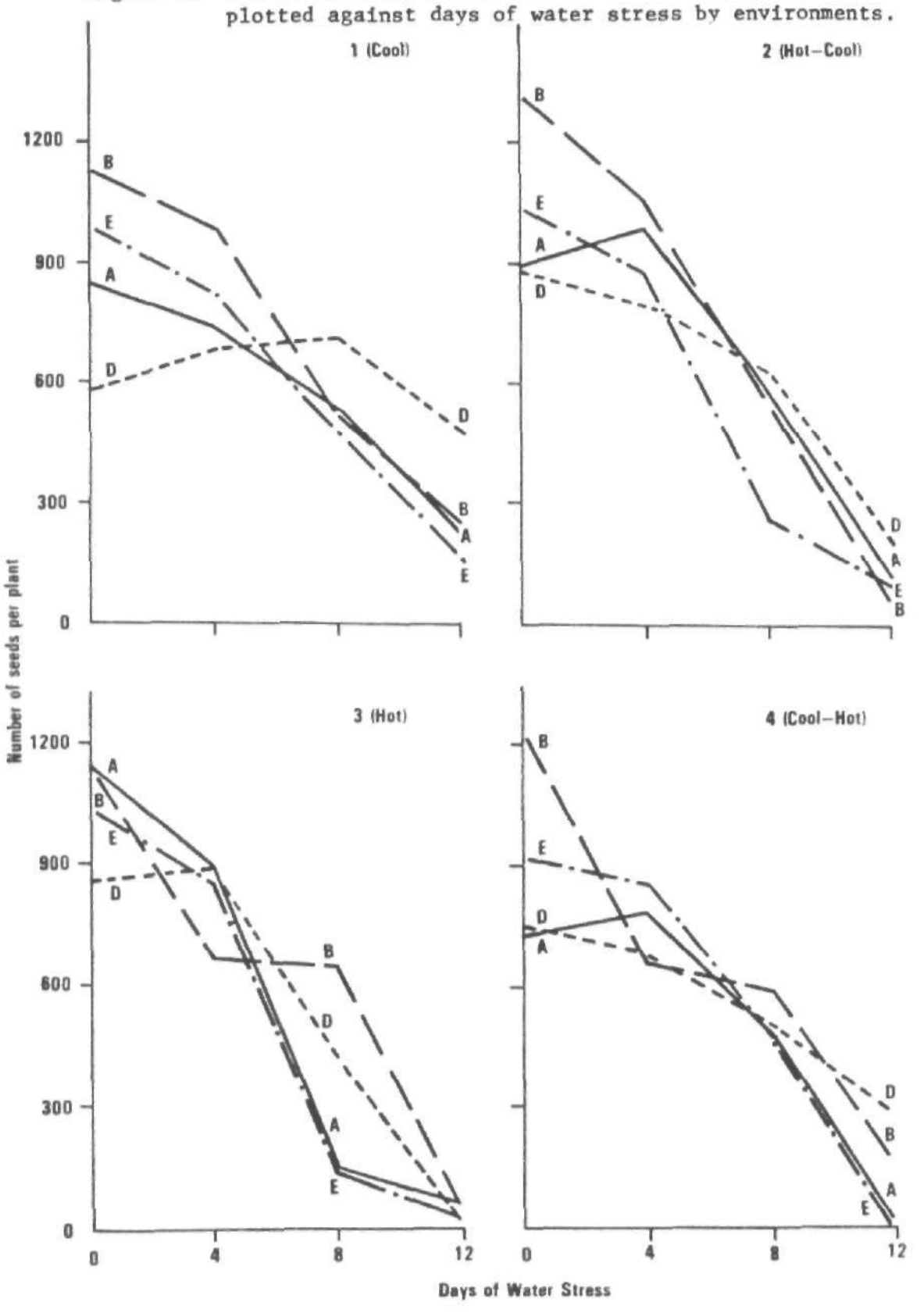
Environment	Seed number(%)	Water stress	Seed number(%)	Genotype	Seed number(%)
1	75	0	114	A	68
2	76	4	98	B	81
3	66	8	57	D	69
4	68	12	16	E	67

all genotypes in all environments. Mild (4 days) water stress had little effect on seed numbers in genotype A in environments 2 and 4 and in genotype D in environment 3.

Under control (non-water stressed) conditions exposure to hign temperatures during panicle initiation and expansion (environments 2 and 3) tended to increase seed numbers for all genotypes except for genotype B which produced slightly more seeds in environment 4 than in environment 3. The greater seed numbers in environments 2 and 3 was due to the larger panicles (see above). The relatively low seed numbers in genotype B under control and mild water stress in environment 3 was probably as a result of heat damage. This genotype was comparatively behind the other genotypes in its development and the second water stress cycle caught it in the late boot stage while other genotypes were in the head emergence or tip-bloom stages of growth. This coupled with the high temperatures in environment 3 led to still higher temperatures in the flag leaf sheaths enclosing the panicles and this may have caused floret abortion.

With the exception of genotype B seed numbers under moderate (8 days) and severe (12 days) water stress were lower in environments 2 and 3 than in environments 1 or 4. In genotype B moderate and severe water stress in environments 2 and 3 caused total or near total damage to the main heads. This caused nodal panicles to be initiated after water stress was relieved but such nodal panicles did not

Figure 7. Number of seeds per plant for four sorghum hybrids plotted against days of water stress by environments.



develop in plants where the damage to the main head was not extreme. These nodal tillers account for the fairly decent seed numbers under moderate water stress in environments 2 and 3 (Tables 12 and 12a, and Fig. 7). Though nodal panicles were also produced by some plants subjected to severe (12 days) water stress the damage to the plants was so severe and recovery so slow that these panicles did not have many grains filled at the time plants were harvested.

When averaged over water stress treatments seed numbers in genotype B were significantly higher than in the three other genotypes in environments 1, 2 and 4. In environment 3 the differences between genotypes were only significant under moderate (8 days) water stress (Tables 12 and 12a). When averaged over all genotypes and all environments seed numbers significantly declined from control (non-water stressed) to severe (12 days) water stress (Tables 12 and 12a).

Seed Size

In general weight of 1000 seeds increased with increased water stress in all environments (Tables 13 and 13a, and Fig. 8). These increases were however not significant except in environment 2. When averaged over all environments seed size was significantly greater under moderate and severe water stress than under control and mild water stress (Tables 13 and 13a).

In environment 1 seed size in genotype A showed a

Table 13. Weight of 1000 seeds (g) for 4 sorghum hybrids grown under four temperature environments and subjected to 2 cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Weight of 1000 Seeds				
1 (Cool)	0	18.1de[1]	27.5abcd	17.3de	24.5abcde	21.8a[2]
	4	16.0e	31.3ab	19.2cde	20.5cde	21.7a
	8	22.6bcde	32.6a	16.1e	28.1abc	24.8a
	12	26.8abcd	---	21.3bcde	31.9ab	26.0a
	mean	20.5c[3]	30.4a	18.3c	25.4b	
2 (Hot--Cool)	0	24.1cd	27.3abcd	26.9abcd	26.8abcd	26.2b
	4	19.1d	31.7abc	26.7abcd	30.5abcd	27.0b
	8	25.1bcd	32.3abc	27.7abcd	32.4abc	29.4b
	12	30.5abcd	---	34.5ab	40.2a	34.8a
	mean	23.4b	30.4a	28.6a	30.7a	
3 (Hot)	0	17.6c	28.4a	20.9bc	24.8ab	22.9a
	4	23.2ab	26.6ab	24.1ab	25.2ab	24.8a
	8	27.8ab	28.0ab	24.7ab	27.5ab	26.8a
	12	---	---	---	---	---
	mean	21.9b	27.6a	23.1b	25.8a	
4 (Cool--Hot)	0	17.7cd	25.1b	18.9bcd	22.8bcd	21.1a
	4	16.2d	32.1a	22.3bcd	20.3bcd	22.7a
	8	22.4bcd	---	22.0bcd	23.4bc	22.6a
	12	---	---	19.6bcd	---	19.6a
	mean	18.8b	28.6a	20.8b	22.1b	

Overall Means

Environment	1000-seed weight	Water stress	1000-seed weight	Genotype	1000-seed weight
1	23.3bc[2]	0	23.0b	A	21.1c
2	28.2a	4	24.0b	B	29.4a
3	24.5b	8	26.0a	D	22.7c
4	22.0c	12	28.1a	E	26.1b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 13a. Weight of 1000 seeds expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	152	96	135	120
	4	88	173	106	113	120
	8	125	180	89	155	137
	12	148	---	118	176	144
	mean	113	168	101	140	
2 (Hot--Cool)	0	133	151	149	148	145
	4	106	175	148	169	149
	8	139	178	153	179	162
	12	169	---	191	222	192
	mean	129	168	158	170	
3 (Hot)	0	97	157	115	137	127
	4	128	147	133	139	137
	8	154	155	136	152	148
	12	---	---	---	---	---
	mean	121	152	128	143	
4 (Cool--Hot)	0	98	139	104	126	117
	4	90	177	123	112	125
	8	124	---	122	129	125
	12	---	---	108	---	108
	mean	104	158	115	122	

Overall Means

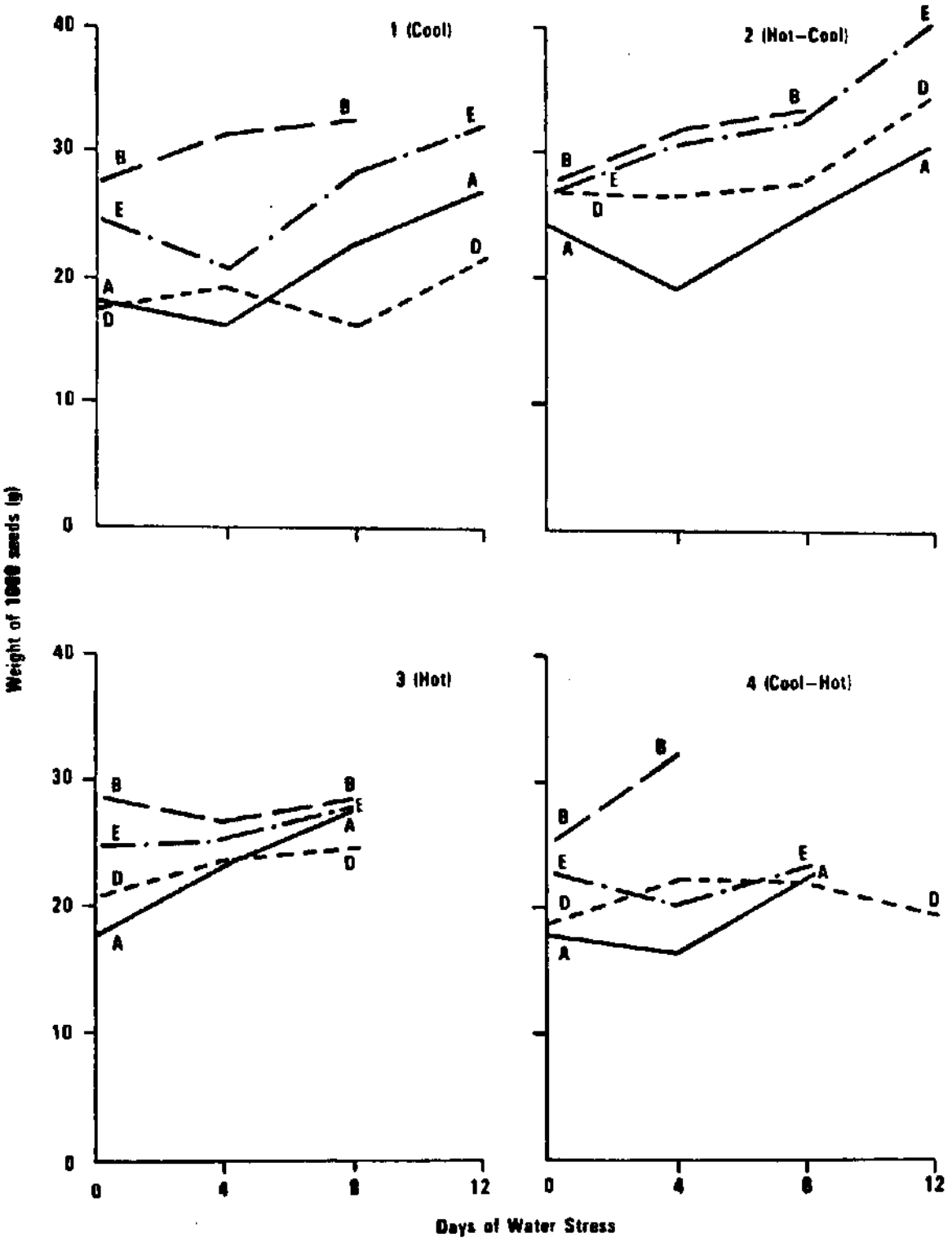
Environment	1000-seed weight(%)	Water stress	1000-seed weight(%)	Genotype	1000-seed weight(%)
1	129	0	127	A	117
2	156	4	133	B	162
3	135	8	144	D	125
4	122	12	155	E	144

slight (12%) decline with mild water stress but it increased over the controls by 25 and 48%, with moderate and severe water stress, respectively. Seed size in genotype B was increased by 14 and 18% by mild and moderate water stress, respectively. With severe water stress there were not enough seeds of genotype B to estimate 1000-seed weight in any of the environments. Seed size in genotype D showed no great or consistent change with water stress in environment 1. In genotype E seed size declined by 16% with mild water stress but increased by 15% with moderate and by 30% with severe water stress (Tables 13 and 13a).

In environment 2 seed size for genotype A again declined with mild water stress (by 21%) but increased by 4 and 27% respectively, with moderate and severe water stress. In genotype B seed size increased by 16 and 18% with mild and moderate water stress, respectively. Seed size in genotype D was not affected except under severe water stress where it increased by 28% over the controls. In genotype E seed size increased by 14, 21, and 50% respectively, with mild, moderate, and severe water stress (Tables 13 and 13a).

In environment 3 only genotype A showed an increase in seed size with increased water stress. In this genotype seed size increased by 31 and 57% with mild and moderate water stress, respectively. All other genotypes showed little or no change in seed size with water stress in this environment (Fig. 8). None of the genotypes produced

Figure 8. Weight of 1000 seeds (g) of 4 sorghum hybrids plotted against days of water stress by environments.



enough seeds under severe water stress for 1000-seed weight determination in environment 3. Even though seed numbers decreased with water stress as in the other environments the high temperatures during grain filling might have limited assimilate transfer to the grains in environment 3 and to some degree in environment 4 under conditions of water stress.

In environment 4 seed size of genotype A was slightly reduced (by 8%) under mild water stress but it increased by 26% with moderate water stress. In genotype B only plants that were well watered (controls) and those subjected to mild water stress produced enough grains for 1000-seed weight determinations. Mild water stress caused a 28% increase in seed size over the controls. In genotypes D and E there was little change in seed size with increase in water stress in environment 4 (Tables 13 and 13a, and Fig. 8).

The slight decreases in seed size of genotype A with mild water stress in environments 2 and 4 was probably because this genotype produced more seeds under mild water stress than under control (well watered) conditions in these environments (See Tables 12 and 13). A decrease in seed size with mild water stress was also observed for genotype E in environment 1. This latter case cannot however be explained by any increase in seed numbers.

In general plants that completed their vegetative and early reproductive phases of growth in the hot environment (environments 2 and 3) had bigger seeds than plants that

completed these phases of growth in the cool environment (environments 1 and 4). The only exception was genotype B which had bigger seeds in the latter environments. This may again have a bearing on the fact that genotype B was generally behind the other three genotypes in its growth and development. Since environments 2 and 3 also had greater seed numbers the larger seeds reflect greater total assimilate availability rather than a compensatory effect due to limitations in sink.

Grain Yield

As would be expected the grain yield per plant reflected the trends in seed numbers and seed size (Tables 14 and 14a, and Fig. 9). Of the two components however, seed number was clearly the more important component determining grain yield in this study. This was because even the large (up to 50% in some cases) increases in seed size were not enough to offset the several fold decreases in seed numbers with increased water stress and with exposure to elevated temperatures under moderate and severe water stress (Tables 12 and 13).

Under control (non-water stressed) conditions genotype B was the highest yielding in all four environments. Even under mild (4 days) water stress genotype B yields were higher than those of the other genotypes in environments 1, 2 and 4. It was however the least stable genotype in all four environments, showing the greatest decline in yield with increase in the length of the water stress period to

Table 14. Grain yield (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Grain Yield				
1 (Cool)	0	15.0cde[1]	30.4a	10.2def	23.8b	19.8a[2]
	4	11.6cdef	28.9ab	13.2cde	16.9c	17.6a
	8	11.8cdef	14.8cde	11.5cdef	12.5cde	12.7b
	12	5.3fg	1.0g	9.1ef	5.1fg	5.1c
	mean	10.9c[3]	18.8a	11.0c	14.5b	
2 (Hot--Cool)	0	21.1cde	35.3a	23.0cde	26.9bc	26.6a
	4	18.7def	32.8ab	21.3cde	25.5cd	24.6a
	8	13.1fg	9.7g	17.1ef	8.5gh	12.1b
	12	1.5i	0.4i	6.4ghi	2.3hi	2.6c
	mean	13.6c	19.5a	17.0ab	15.8bc	
3 (Hot)	0	19.5cd	31.8a	18.0cd	25.5b	23.7a
	4	19.5cd	16.9cd	21.3bc	21.6bc	19.8a
	8	3.6ef	14.1d	7.4e	4.1ef	7.3b
	12	1.4f	0.4f	0.0f	1.7f	0.9c
	mean	11.0b	15.8a	11.7b	13.2b	
4 (Cool--Hot)	0	12.6cde	29.9a	14.8cd	20.6b	19.5a
	4	12.2de	20.9b	14.6cde	17.2bc	16.2a
	8	10.3de	13.0cde	9.8e	10.4de	11.1b
	12	0.2f	2.3f	4.7f	0.0f	1.8c
	mean	8.8c	16.5a	11.0bc	12.0b	

Overall Means

Environment	Grain yield	Water stress	Grain yield	Genotype	Grain yield
1	13.8ab[2]	0	22.4a	A	11.1c
2	16.5a	4	19.6b	B	17.7a
3	12.9ab	8	10.7c	D	12.6b
4	12.2b	12	2.6d	E	13.9b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 14a. Grain yield per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	203	68	159	132
	4	77	193	88	113	117
	8	79	99	77	83	85
	12	35	7	61	34	34
	mean	73	125	73	97	
2 (Hot--Cool)	0	141	235	153	179	177
	4	125	219	142	170	166
	8	87	65	114	57	81
	12	10	3	43	15	17
	mean	91	130	113	105	
3 (Hot)	0	130	212	120	170	158
	4	130	113	142	144	132
	8	24	94	49	27	49
	12	9	3	0	11	6
	mean	73	105	78	88	
4 (Cool--Hot)	0	84	199	99	137	130
	4	81	139	87	115	108
	8	69	87	73	69	74
	12	1	15	31	0	12
	mean	59	110	73	80	

Overall Means

Environment	Grain yield(%)	Water stress	Grain yield(%)	Genotype	Grain yield(%)
1	92	0	149	A	74
2	110	4	131	B	118
3	86	8	71	D	84
4	81	12	17	E	93

8 and 12 days (Tables 14 and 14a, and Fig. 9).

Genotype E was the second highest yielding under non-water stressed and mildly water stressed conditions in all the environments but like genotype B its grain yield greatly declined with moderate and severe water stress (Tables 14 and 14a, and Fig. 9).

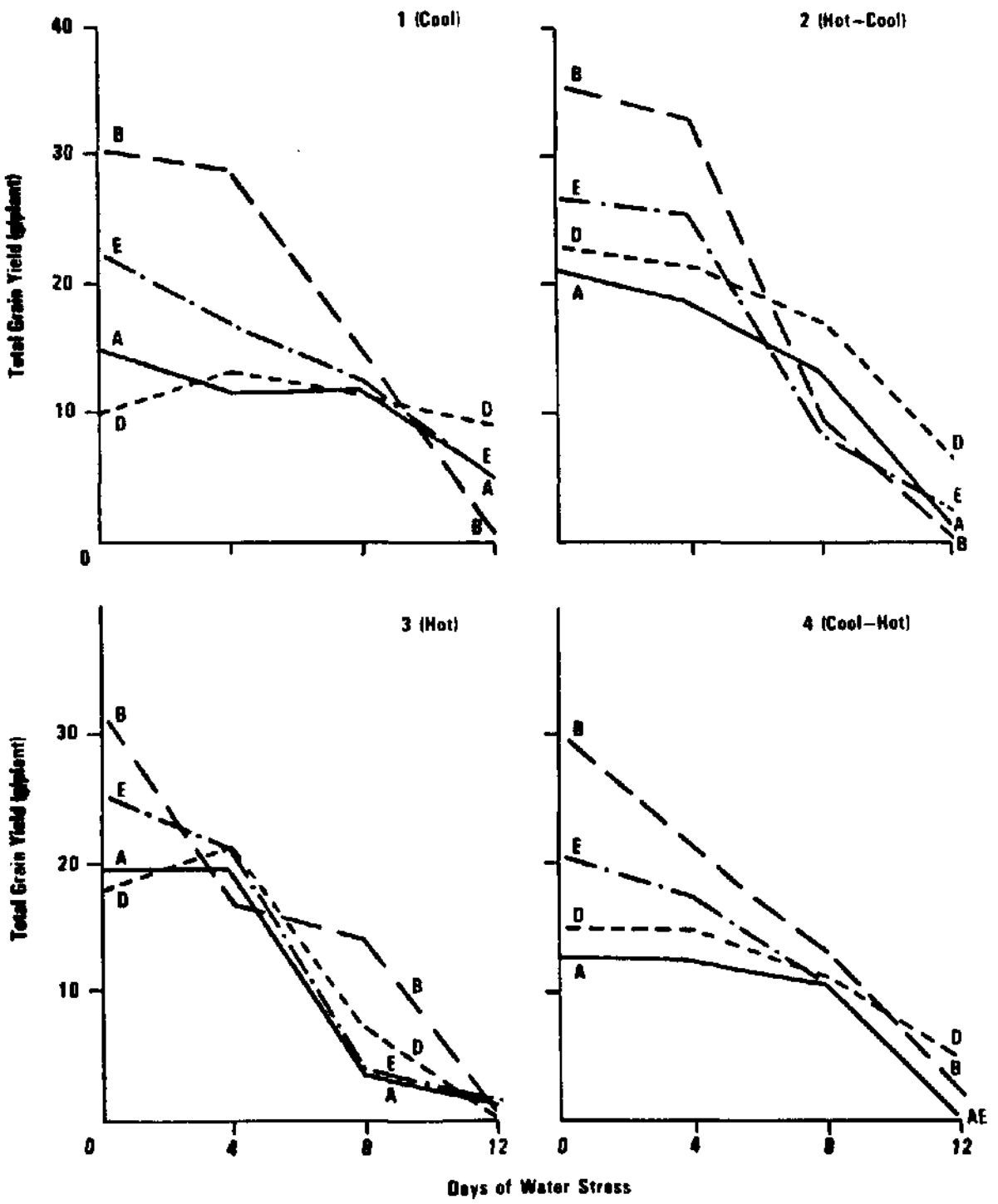
Genotype D showed the greatest stability in yield across water stress treatments in environments 1, 2 and 4. In environment 3 where high temperatures accompanied both cycles of water stress genotype D fared no better than the other genotypes in terms of yield stability.

Genotype A was the lowest yielding of the four especially under non-water stressed and mildly water stressed conditions, but showed less decrease in yield with mild and moderate water stress in environments 1, 2 and 4. Except in environment 1 severe water stress caused a sharp decline in the grain yield of genotype A.

Under control (non-water stressed) conditions all genotypes gave higher grain yields in environments 2 and 3 than in environments 1 and 4. As stated earlier this was due to higher seed numbers from the larger panicles in the two former environments. This was also true under mild water stress, except for genotype B which gave higher grain yields in environments 1 and 4 than it did in environment 3.

Significant differences were observed in the average grain yield between environments, water stress treatments and genotypes.

Figure 9. Grain yield (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments.



Leaf Dry Matter

Leaf dry matter per plant is presented in Tables 15 and 15a. Significant differences in leaf dry matter were observed between genotypes in all environments. Only severe (12 days) water stress in environments 2 and 3 caused significant decreases in leaf weights from those of controls (non-water stressed). There were significant differences in leaf weight between environments 1 and 2, 1 and 3, and 3 and 4. Differences between environments 1 and 4, 2 and 3, and 2 and 4 were not significant (Tables 15 and 15a).

Stem Dry Matter

As with leaf dry matter significant genotypic differences were observed in stem dry matter in all environments (Tables 16 and 16a). Similarly only 12 days of water stress in environments 2, 3 and 4 caused a significant decline in stem dry matter from those of the controls. Differences in stem dry matter between environments were not significant.

Total Dry Matter

This included all above ground plant parts and is presented in Tables 17 and 17a and plotted against days of water stress in Figure 10. As with grain yield total dry matter production was highest for genotype B in all environments but its productivity rapidly declined with increasing

Table 15. Leaf dry matter (g per plant) for four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Leaf Dry Matter				
1 (Cool)	0	6.0def[1]	9.3b	4.8gh	7.7c	7.0a[2]
	4	5.6efg	9.1b	5.2fgh	7.3cd	6.8a
	8	5.3fgh	10.0ab	5.3fgh	7.3cd	7.0a
	12	5.3fgh	10.8a	4.3h	5.9def	6.6a
	mean	5.6c[3]	9.8a	4.9d	7.1b	
2 (Hot--Cool)	0	7.5de	9.8ab	6.5e	8.5bcd	8.1a
	4	7.1de	9.4bc	5.9ef	8.6bcd	7.7ab
	8	7.1de	11.4a	5.8ef	7.7cde	8.0ab
	12	6.1ef	8.5bcd	4.6f	6.9de	6.5b
	mean	7.0c	9.8a	5.7d	7.9b	
3 (Hot)	0	7.7bcd	10.2a	6.3def	8.6b	8.2a
	4	8.1bc	10.7a	6.3def	8.0bcd	8.3a
	8	7.7bcd	11.4a	5.6ef	7.2bcde	8.0a
	12	6.3def	8.1bc	4.7f	6.6cdef	6.4b
	mean	7.5b	10.1a	5.7c	7.6b	
4 (Cool--Hot)	0	6.1de	10.5ab	5.2efg	7.8c	7.4a
	4	6.3de	9.7b	5.6ef	7.1cd	7.2a
	8	5.7ef	10.9a	4.6fg	7.2cd	7.1a
	12	5.8e	9.8ab	4.3g	6.3de	6.6a
	mean	6.0c	10.2a	4.9d	7.1b	

Overall Means

Environment	Leaf dry matter	Water stress	Leaf dry matter	Genotype	Leaf dry matter
1	6.9c[2]	0	7.7a	A	6.5c
2	7.6ab	4	7.5a	B	10.0a
3	7.7a	8	7.5a	D	5.3d
4	7.1bc	12	6.5b	E	7.4b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 15a. Leaf dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	155	80	128	117
	4	93	152	87	122	113
	8	88	167	88	122	117
	12	88	180	72	98	110
	mean	93	163	82	118	
2 (Hot--Cool)	0	125	163	108	142	135
	4	118	157	98	142	128
	8	118	190	97	128	133
	12	102	142	77	115	108
	mean	117	163	95	132	
3 (Hot)	0	128	170	105	143	137
	4	135	178	105	133	138
	8	128	190	93	120	133
	12	195	135	78	110	107
	mean	125	168	95	127	
4 (Cool--Hot)	0	102	175	87	130	123
	4	105	162	93	118	120
	8	95	182	77	120	118
	12	97	163	72	105	110
	mean	100	170	82	118	

Overall Means

Environment	Leaf dry matter(%)	Water stress	Leaf dry matter(%)	Genotype	Leaf dry matter(%)
1	115	0	128	A	108
2	127	4	125	B	167
3	128	8	125	D	88
4	118	12	108	E	123

Table 16. Stem dry matter (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress days	Genotype A	B	D	E	Mean
		Stem Dry Matter				
1 (Cool)	0	11.3def[1]	23.9a	8.1f	17.3bc	15.2a[2]
	4	9.3ef	23.8a	9.7ef	13.8cde	14.2a
	8	9.5ef	25.4a	8.6f	15.5cd	14.8a
	12	9.1ef	22.1ab	6.7f	8.8f	11.7a
	mean	9.8c[3]	23.8a	8.3c	13.9b	
2 (Hot--Cool)	0	13.9efg	23.7bc	12.4fg	19.4cde	17.4a
	4	13.0efg	28.2ab	13.5efg	21.7cd	19.1a
	8	13.9efg	30.8a	9.8gh	16.7def	17.8a
	12	10.0gh	16.2defg	4.9h	11.4fg	10.7b
	mean	12.7c	24.8a	10.2c	17.3b	
3 (Hot)	0	12.4cd	27.2a	11.6de	19.4b	17.7a
	4	17.9bc	30.1a	13.2cd	17.5bc	19.7a
	8	12.5cd	29.5a	10.6def	13.7bcd	16.6a
	12	6.2ef	10.7def	5.3f	6.5ef	7.2b
	mean	12.3bc	24.4a	10.2c	14.3b	
4 (Cool--Hot)	0	8.9de	27.1a	10.1de	16.2bc	15.6a
	4	10.1de	25.7a	10.6de	14.2bcd	15.2a
	8	9.8de	25.2a	9.5de	13.6cd	14.5a
	12	7.9e	19.1b	6.2e	7.7e	10.2b
	mean	9.2c	24.3a	9.1c	12.9b	

Overall Means

Environment	Stem dry matter	Water stress	Stem dry matter	Genotype	Stem dry matter
1	14.0a[2]	0	16.5a	A	11.0c
2	16.3a	4	17.1a	B	24.3a
3	15.3a	8	15.9a	D	9.5d
4	13.9a	12	9.9b	E	14.6b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 16a. Stem dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	212	72	153	135
	4	82	211	86	122	126
	8	84	225	76	137	131
	12	81	196	59	78	104
	mean	87	211	73	123	
2 (Hot--Cool)	0	123	210	110	172	154
	4	115	250	119	192	169
	8	123	273	87	148	158
	12	89	143	43	101	95
	mean	112	219	90	153	
3 (Hot)	0	110	241	103	172	157
	4	158	266	117	155	174
	8	111	261	94	121	147
	12	55	95	47	58	64
	mean	109	216	90	127	
4 (Cool--Hot)	0	79	240	89	143	138
	4	89	227	94	126	135
	8	87	223	84	120	128
	12	70	169	55	68	90
	mean	81	215	81	114	

Overall Means

Environment	Stem dry matter(%)	Water stress	Stem dry matter(%)	Genotype	Stem dry matter(%)
1	124	0	146	A	97
2	144	4	151	B	215
3	135	8	141	D	84
4	123	12	88	E	129

Table 17. Total plant dry matter (g per plant) for 4 sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Total Dry Matter				
1 (Cool)	0	38.3cdef[1]	76.2a	27.6efg	58.6b	50.2a[2]
	4	31.6defg	72.9a	33.9defg	46.2c	46.2ab
	8	31.6defg	58.7b	30.0efg	42.4cd	40.7b
	12	27.0fg	39.1cde	24.7g	27.9efg	29.7c
	mean	32.1c[3]	61.7a	29.1c	43.8b	
2 (Hot--Cool)	0	50.4cd	82.3a	49.8cd	65.6b	62.0a
	4	47.0d	82.7a	48.2cd	66.7b	61.2a
	8	41.2de	59.6bc	39.7def	43.6d	46.0b
	12	25.0g	30.3efg	18.7g	28.5fg	25.6c
	mean	40.9c	63.7a	39.1c	51.1b	
3 (Hot)	0	46.3defg	79.8a	42.0efgh	61.6bc	57.4a
	4	53.5cde	67.3b	47.9def	54.5cd	55.8a
	8	35.1ghi	65.4bc	33.2hi	38.7fgh	43.1b
	12	19.7ik	26.0ii	13.3k	36.9fghi	24.0c
	mean	38.7c	59.6a	34.1c	47.9b	
4 (Cool--Hot)	0	32.2fghi	77.6a	35.7fg	52.2cd	49.4a
	4	34.0fgh	65.0b	36.1fg	46.7de	45.5a
	8	32.7fghi	57.9bc	30.2ghij	40.9ef	40.4a
	12	22.6ij	37.1efg	20.5i	25.2hij	26.4b
	mean	30.4c	59.4a	30.6c	41.3b	

Overall Means

Environment	Total dry matter	Water stress	Total dry matter	Genotype	Total dry matter
1	41.7b[2]	0	54.8a	A	35.5c
2	48.7a	4	52.1a	B	61.1a
3	45.1ab	8	42.6b	D	33.2c
4	40.4b	12	26.4c	E	46.0b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

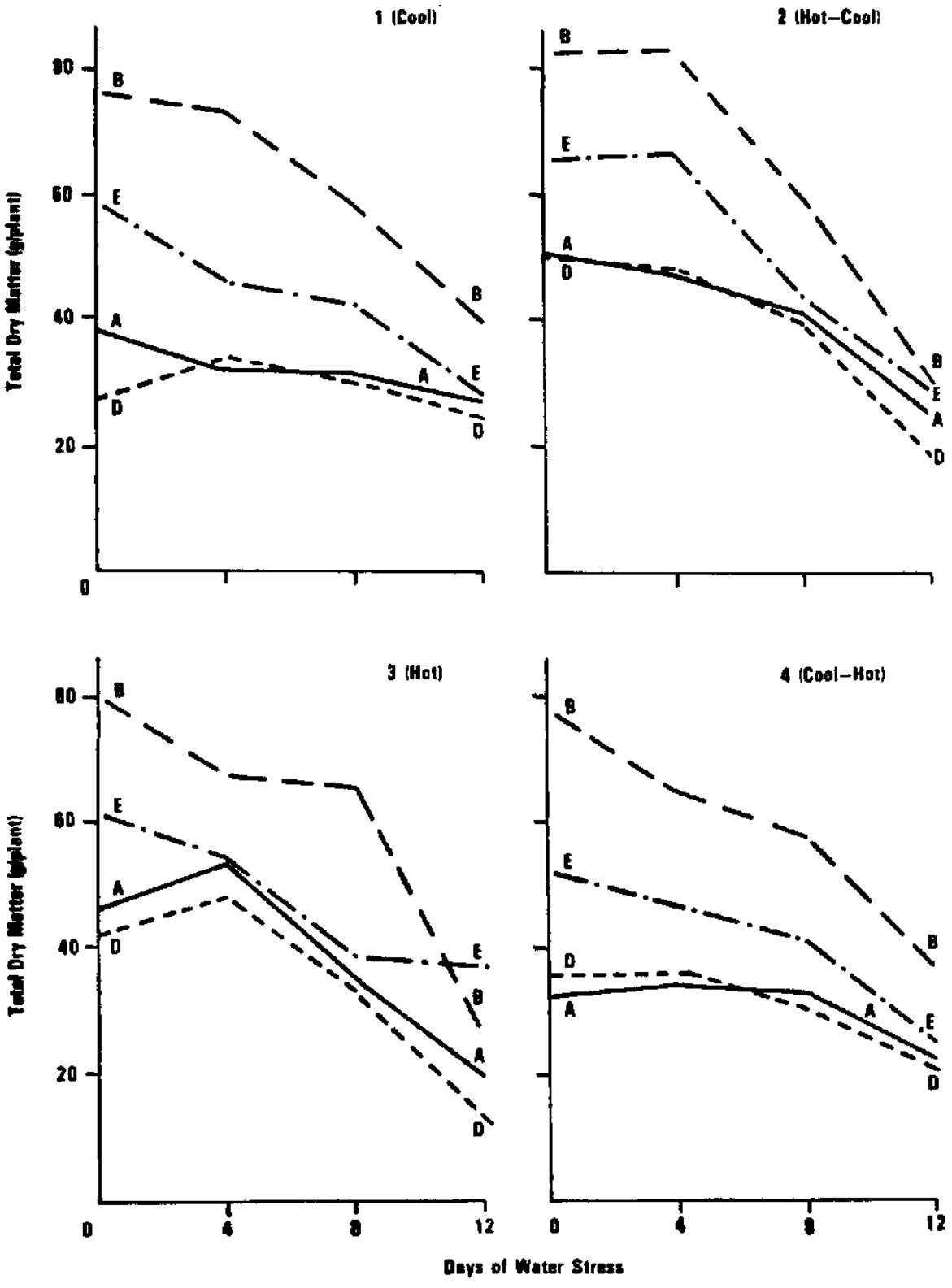
Table 17a. Total dry matter per plant expressed as percentages of genotype A, water stress 0, environment 1.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent				
1 (Cool)	0	100	199	72	153	131
	4	83	190	89	121	121
	8	83	153	78	111	106
	12	70	102	64	73	78
	mean	84	161	76	114	
2 (Hot--Cool)	0	132	215	130	171	162
	4	123	216	126	174	160
	8	108	156	104	114	120
	12	65	79	49	74	67
	mean	107	166	102	133	
3 (Hot)	0	121	208	110	161	150
	4	140	176	125	142	146
	8	92	171	87	101	113
	12	51	68	35	96	63
	mean	101	156	89	126	
4 (Cool--Hot)	0	84	203	93	136	129
	4	89	170	94	122	119
	8	85	151	79	107	105
	12	59	97	54	66	69
	mean	79	155	80	108	

Overall Means

Environment	Total dry matter(%)	Water stress	Total dry matter(%)	Genotype	Total dry matter(%)
1	109	0	143	A	93
2	127	4	136	B	160
3	118	8	111	D	87
4	105	12	69	E	120

Figure 10. Total dry matter (g per plant) of 4 sorghum hybrids plotted against days of water stress by environments.



water stress. Genotypes A and D were the lowest but they showed the greatest stability across water stress treatments (Tables 17 and 17a, and Fig. 9).

Under control (non-water stressed) and mildly water stressed conditions the highest biological productivity was again obtained in environments 2 and 3. Mild water stress did not cause a significant decrease in total dry matter in any of the environments but moderate water stress except in environment 4, and severe water stress caused significant decreases in total dry matter in all environments and across environments (Tables 17 and 17a).

Interactions of Environment, Water Stress, and Genotype

The two-way and three-way interactions between environment, water stress, and genotype for the various plant parameters measured are presented in Table 18.

Environment x Water Stress

Except for 1000-seed weight, leaf dry matter and stem dry matter this interaction was significant indicating that the differential response of the various parameters measured to water stress in different environments were significant. This interaction was not significant in the case of 1000-seed weight because differences between water stress treatments were not significant in three of the four environments, and in the fourth environment only severe water stress was significantly different from the other three water stress

Table 18. Interactions between environment, water stress, and genotype for the various plant parameters measured in experiment 1.

	Interaction Term			
Parameter	Environment x Water stress	Environment x Genotype	Water stress x Genotype	Environment x Water stress x Genotype
Plant height	* *	*	*	*
Panicle weight	*	NS	*	*
Number of seeds	*	NS	*	*
1000-seed weight	NS	NS	NS	NS
Grain yield	*	NS	*	*
Leaf dry matter	NS	*	*	NS
Stem dry matter	NS	NS	*	NS
Total dry matter	*	NS	*	*

* Denotes significance at p = .05.
NS = Not significant

treatments (Tables 13 and 13a). Similarly only severe water stress caused a significant decrease in leaf and stem dry matter (Tables 15, 15a, 16, and 16a).

Environment X Genotype

Significant environment x genotype interactions were observed only in plant height and leaf dry matter. This interaction term was significant for plant height because of the marked differences in the response of the four genotypes to water stress in the different environments. Genotype B which was the tallest under control (non-water stressed) conditions in environments 1 and 4 was drastically reduced in height by both water stress and exposure to high temperatures during the vegetative phase of growth (environments 2 and 3), while plant height in genotype D was almost unaffected by water stress in environments 1 and 4 and only reduced in environments 2 and 3 when subjected to severe (12 days) water stress. Furthermore, plant height in genotype D was actually increased under control and mild water stress by exposure to high temperatures during the vegetative phase of growth (Tables 10 and 10a). Similarly leaf dry matter in genotypes B and E did not change appreciably from one environment to another but in genotypes A and D leaf dry matter showed a substantial increase due to exposure to high temperatures during the vegetative phase of growth (Tables 15 and 15a).

Water Stress X Genotype

Only 1000-seed weight did not show significance for this interaction. As earlier stated though differences in seed weight between water stress treatments were significant when averaged over environments, they were not significant in the individual environments. For all the other parameters the significance of this interaction reflects the differential response of the genotypes to water stress (Tables 10 through 17a).

Environment X Water Stress X Genotype

As would be expected this three-way interaction was significant whenever more than one of the three two-way interactions were significant (Table 18).

Heat and Desiccation Tolerance Tests

These tests were conducted to evaluate the degree of membrane stability as measured by electrolyte leakage from the leaf discs. The degree of membrane stability has been found to correlate well with tolerance of other plant processes to stress (Sullivan and Ross, 1979).

The tests in this study were conducted on different days for each water stress treatment and the control (non-water stressed) plants were tested each time one of the water stress treatments was tested. Because there were too many factors that could cause significant variations in the measured percentage injury from one sampling date to another

comparisons between water stress treatments was not feasible, despite the various precautions taken to minimize these variations: Number of washings and amount of water used per washing; heating temperature and length of heating—a very small change in temperature at about the 50% injury level may cause large changes in the injury (Sullivan, 1972). Furthermore because of the differences in the lengths of the water stress periods there were as many as 13 and 11 days, respectively, for the first and second sets of tests between the ages of plants subjected to 4 and 12 days of water stress at the respective times of sampling.

The first set of tests were conducted between panicle initiation and the boot stage before half the total number of plants in each greenhouse bay was moved from one bay to the other. At such there were only two environments [cool (1) and hot (3)] for these tests.

Heat and desiccation tolerance tests were conducted on leaf discs of plants subjected to 4 days of water stress, after a 6-day recovery period from the end of the first water stress cycle. The results are given in Tables 19 and 19a, respectively. From the preceeding discussion 4 days of water stress generally had little effect on most of the parameters measured except in genotype B and in environment 3 where plants were exposed to high temperatures throughout their growth. From the results in Tables 19 and 19a however, it is clear that there were differences in the degree of membrane stability between the control (non-water stressed)

Table 19. Percentage injury to leaf discs of control and mildly water stressed plants sampled 45 days after emergence and heated at 53.5 C.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent Injury				
1 (Cool)	0	53.5abc[1]	64.6ab	72.0a	59.1abc	62.6a[2]
	4	31.3c	46.7abc	48.7abc	43.0bc	42.4b
	mean	42.4a[3]	55.6a	60.4a	49.4a	
3 (Hot)	0	27.0cd	55.0a	58.4a	36.5bc	44.2a
	4	19.0d	27.5cd	42.6b	21.2d	27.5b
	mean	28.8c	41.2b	50.5a	23.0c	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	52.1a[2]	0	53.0a	A	32.7b
3	35.9a	4	35.0b	B	48.4a
				D	55.4a
				E	38.2b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 19a. Percentage injury to leaf discs of control and mildly water stressed plants sampled 45 days after emergence and desiccated at -16 bars with PEG.

Environment	Water stress(days)	Genotype A	B	D	E	Mean
		Percent Injury				
1 (Cool)	0	32.5cd[1]	50.6a	38.9bc	44.9ab	41.4a[2]
	4	23.4d	29.9cd	27.9d	39.3bc	30.1b
	mean	28.0c[3]	40.3ab	33.4bc	41.5a	
3 (Hot)	0	30.1bc	33.9abc	38.4ab	44.9a	36.8a
	4	21.1c	23.2c	30.6abc	32.4abc	26.8b
	mean	25.6b	28.6b	34.5ab	38.6a	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	35.7a[2]	0	39.0a	A	26.8c
3	31.8a	4	28.5b	B	34.4ab
				D	33.9b
				E	39.9a

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

and 4-days water stressed plants. In both tables it is shown that leaf discs from the plants subjected to 4 days of water stress were injured significantly less than those of the controls in both environments and when averaged over environments.

Though differences in percent injury between the two environments were not significant for either of the two tests the average percentage injury was lower for environment 3 for both tests indicating a certain degree of "hardening" due to growth under elevated temperatures.

In most of the preceeding discussion genotypes B and E were shown to be susceptible to both water stress and exposure to high temperatures and genotypes A and D were tolerant of water stress and elevated temperatures when the water stress period was 8 days or less. This is supported by the results of the desiccation tolerance test (Table 18a) where genotypes B and E were injured significantly more than genotypes A and D. Percent injury due to heat was, however, greater for genotypes B and D than for genotypes A and E (Table 19).

Because greater genotypic differences in percent injury were observed in the desiccation tolerance tests and the widest average variation was between genotypes A and E (See Table 19a) these two were chosen for the desiccation tolerance tests on the plants subjected to 8 days of water stress. This test was also conducted after a 6-day recovery period from the end of the first water stress cycle. Once

Table 20. Percentage injury to leaf discs of control and moderately water stressed plants sampled 49 days after emergence and desiccated at -16 bars with PEG.

Environment	Water stress (days)	Genotype A	Genotype E	Mean
		Percent Injury		
1 (Cool)	0	32.8b[1]	38.8a	35.8a[2]
	8	24.3c	31.2b	27.8b
	mean	28.6b[3]	35.0a	
3 (Hot)	0	27.9ab	30.3a	29.1a
	8	24.0bc	23.4c	23.7b
	mean	26.0a	26.8a	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	31.8a[2]	0	32.4a	A	27.3b
3	26.4a	8	25.7b	E	30.9a

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

again the water stressed plants showed significantly less injury in both environments and when averaged over environments (Table 20). Differences in percent injury between environments were again not significant but leaf discs from environment 3 plants were injured 20% less than those from environment 1 plants. Genotype E was injured more than genotype A in both environments but the difference was significant only in environment 1 and when averaged over environments (Table 20).

Table 21 gives results of heat and Table 21a desiccation tolerance tests conducted on leaf discs of plants subjected to 12 days of water stress. These tests were conducted after a 9-day recovery period from the end of the first cycle of water stress. Injury from both tests were significantly lower for leaf discs from the water stressed plants and for those from environment 3 plants than for those from environment 1 plants. In the heat tolerance test on environment 1 plants genotype B was injured significantly more than genotypes A and D but genotype E was injured significantly less than A and D. In environment 3 differences in percent injury were significant only between genotypes A and E (Table 21).

Results of the desiccation tolerance test (Table 21a) followed the same general trend except that the percent injury for genotypes B and E were consistently and significantly greater than for genotypes A and D.

Table 21. Percentage injury to leaf discs of control and severely water stressed plants sampled 56 days after emergence and heated at 53.5 C.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Percent Injury				
1 (Cool)	0	71.9bcd[1]	84.8a	74.7abc	61.5def	73.2a[2]
	12	59.6ef	78.1ab	65.8cde	52.8f	64.1b
	mean	65.8b[3]	81.5a	70.3b	57.2c	
3 (Hot)	0	64.5a	61.3a	63.8a	54.0ab	60.9a
	12	52.1ab	45.6b	45.1b	42.0b	46.2b
	mean	58.4a	53.4ab	54.5ab	48.0b	

Overall Means

Environment	Percent injury	Water stress	percent injury	Genotype	Percent injury
1	68.7a[2]	0	67.1a	A	62.1a
3	53.6a	12	55.1b	B	67.4a
				D	62.4a
				E	52.6b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 21a. Percentage injury to leaf discs of control and severely water stressed plants sampled 56 days after emergence and desiccated at -16 bars with PEG.

Environment	Water stress (days)	Genotype A	B	D	E	Mean
		Percent Injury				
1 (Cool)	0	34.1c[1]	46.5a	31.8c	44.0ab	39.1a[2]
	12	28.9c	36.8bc	29.8c	36.0bc	32.9b
	mean	31.5b[3]	41.7a	30.8b	40.0a	
3 (Hot)	0	26.4bc	32.5a	24.9bcd	29.3ab	28.3a
	12	20.2d	23.2cd	22.6cd	24.1bcd	22.6b
	mean	23.3b	27.9a	23.8b	26.7ab	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	36.0a[2]	0	33.7a	A	27.4b
3	25.4b	12	27.7b	B	34.8a
				D	27.3b
				E	33.4a

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Because of leaf senescence at the end of the second water stress cycle, and thus lack of enough leaf area from which to sample leaf discs, the desiccation tolerance tests were not conducted during the second set of tests. Heat tolerance tests were conducted after recovery periods of 5, 8, and 10 days from the end of the second water stress cycle, on plants stressed for 4, 8, and 12 days, respectively. Because of advanced leaf senescence under 12 days of water stress in environments 3 and 4 the tests were conducted on plants in environments 1 and 2 only, under this level of water stress.

The results of heat tolerance tests on plants subjected to 4, 8, and 12 days of water stress are presented in Tables 22, 23, and 24, respectively. As in the previous set of tests leaf discs from water stressed plants were consistently injured less than those from control plants in all environments though these differences were only significant for the plants subjected to 8 and 12 days of water stress. In the plants subjected to 4 days of water stress, genotype E was consistently injured more than genotype A but the differences were not significant (Table 22). This trend was reversed in plants subjected to 8 and 12 days of water stress, and genotype E was injured less than genotype A though the differences were significant only when averaged over environments in the case of plants subjected to 8 days of water stress, and in environment 2 and when averaged over environments in the case

Table 22. Percentage injury to leaf discs of control and mildly water stressed plants sampled 68 days after emergence and heated at 53.5 C.

Environment	Water stress(days)	Genotype A	Genotype E	Mean
		Percent Injury		
1 (Cool)	0	39.0a[1]	42.5a	40.7a[2]
	4	29.0a	34.4a	31.7b
	mean	34.0a[3]	38.5a	
2 (Hot--Cool)	0	34.0a	36.7a	35.4a
	4	26.3a	31.0a	28.7a
	mean	30.2a	33.9a	
3 (Hot)	0	30.0a	33.6a	31.8a
	4	19.1a	26.8a	23.0a
	mean	24.6a	30.2a	
4 (Cool--Hot)	0	37.0a	40.5a	38.7a
	4	33.9a	35.0a	34.5a
	mean	35.5a	37.8a	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	36.2a[2]	0	36.7a	A	31.0a
2	32.0ab	4	29.0a	E	35.1a
3	27.4b				
4	36.6a				

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 23. Percentage injury to leaf discs of control and moderately water stressed plants sampled 75 days after emergence and heated at 53.5 C.

Environment	Water stress (days)	Genotype A	Genotype E	Mean
		Percent Injury		
1 (Cool)	0	76.3a[1]	74.2a	75.3a[2]
	8	61.7ab	53.6b	57.7b
	mean	69.0a[3]	63.9a	
2 (Hot--Cool)	0	53.0a	46.0ab	49.5a
	8	35.4bc	28.3c	31.9a
	mean	44.2a	37.1a	
3 (Hot)	0	57.1a	54.1a	55.6a
	8	11.1b	9.0b	10.0b
	mean	34.1a	31.5a	
4 (Cool--Hot)	0	68.3a	58.4ab	63.4a
	8	45.5bc	32.2c	38.9a
	mean	56.9a	45.3a	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	66.5a[2]	0	60.9a	A	51.1a
2	40.7ab	8	34.6b	E	44.5b
3	32.8b				
4	51.1ab				

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same row followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

Table 24. Percentage injury to leaf discs of control and severely water stressed plants sampled 81 days after emergence and heated at 53.5 C.

Environment	Water stress(days)	Genotype A	Genotype E	Mean
		Percent Injury		
1 (Cool)	0	54.6a[1]	41.8ab	48.2a[2]
	12	34.0ab	22.5b	28.2b
	mean	44.3a[3]	32.2a	
2 (Hot--Cool)	0	37.9a	33.2a	35.6a
	12	21.1b	11.0c	16.1b
	mean	29.5a	22.1b	

Overall Means

Environment	Percent injury	Water stress	Percent injury	Genotype	Percent injury
1	38.2a[2]	0	41.8a	A	36.9a
2	25.8b	12	22.1b	E	27.1b

[1] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05,

[2] Means in the same column followed by the same letter(s) are not significantly different at p = .05,

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05, by Duncan's New Multiple Range Test.

of plants subjected to 12 days of water stress (Tables 23 and 24). It is possible that a combination of plant age, extended water stress and exposure to elevated temperatures eliminated the genotypic differences in the degree of membrane thermostability.

There were significant differences in % injury between environments in the tests on all three levels of water stress. Since no significant genotype x environment interactions were observed in any of the tests the percent injury was averaged over genotypes and plotted against cumulative growing degree days in Figures 11 and 12, for the tests on plants subjected to 4 and 8 days of water stress, respectively.

$$\text{Cumulative GDD} = \sum_{E}^{S} \text{Integrated average daily temperature(F)-50F}$$

Where GDD is growing degree days

E is emergence date

S is sampling date

and 50F is the base temperature for a warm season crop (Neild et al., 1978).

Both Figures 11 and 12 show a significant negative linear correlation between cumulative growing degree days and percent injury to leaf discs.

Under 12 days of water stress leaf discs from plants that were exposed to high temperature up to the boot stage still showed significantly less injury than those from plants that remained in the cool environment throughout

Figure 11. Percentage injury to sorghum leaf discs versus cumulative growing degree days for control and 4 days water stressed plants sampled 68 days after emergence. Treatment temperature was 53.5 C for 15 minutes.

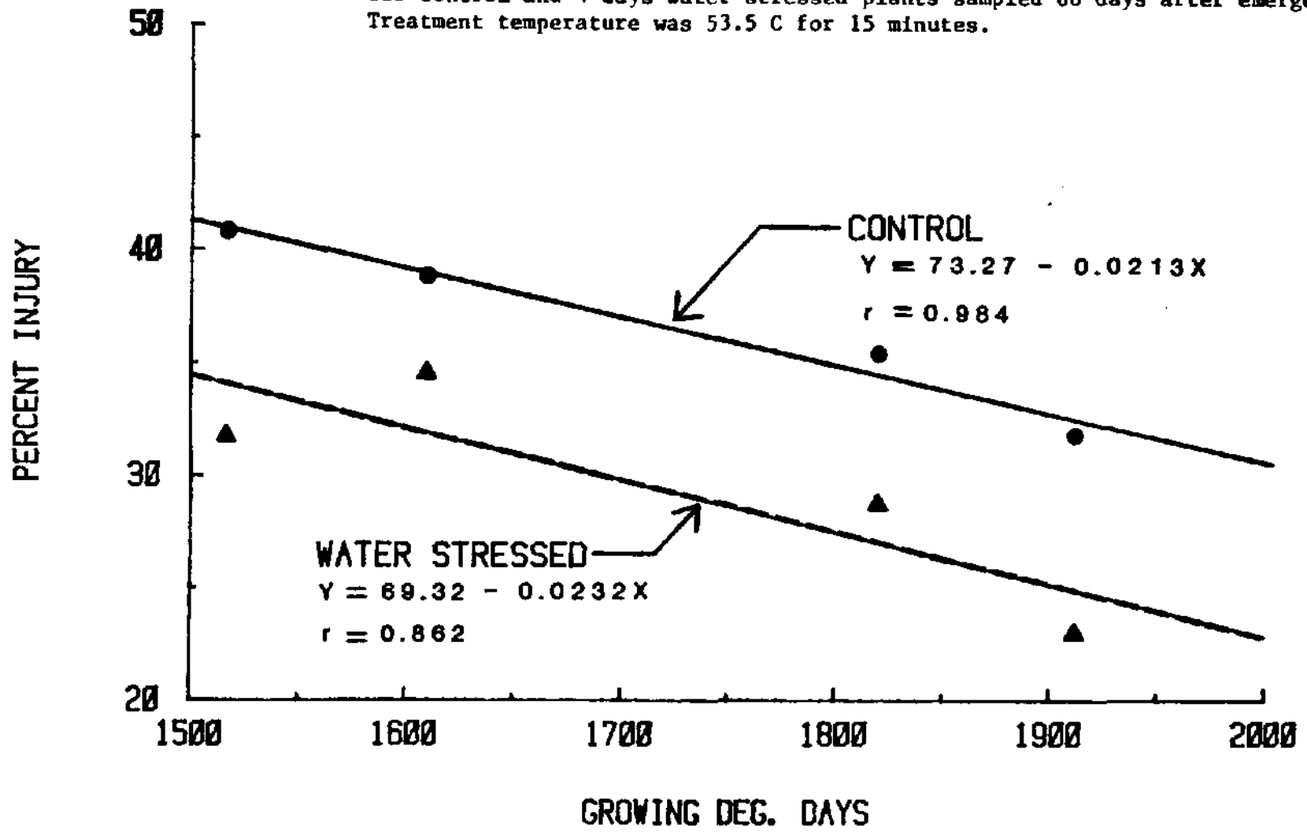
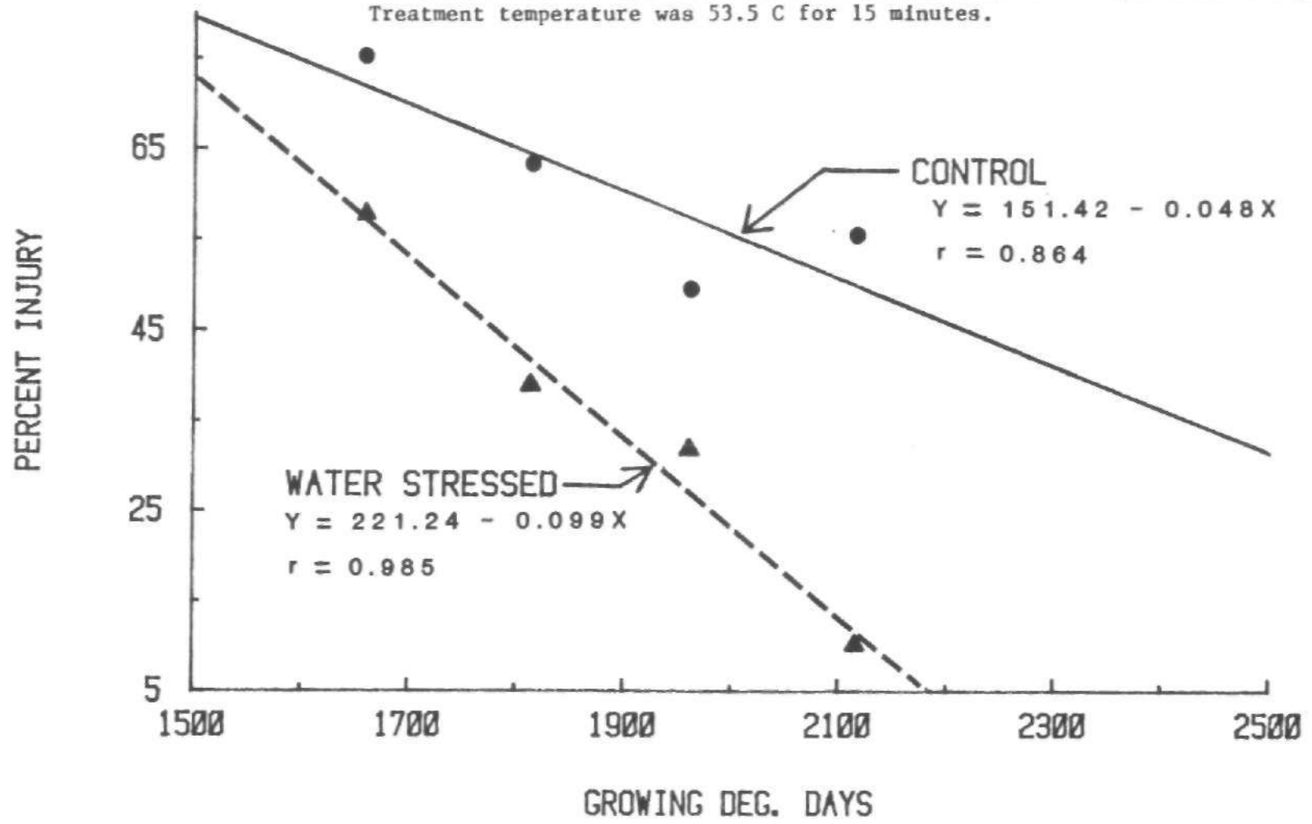


Figure 12. Percentage injury to sorghum leaf discs versus cumulative growing degree days for control and 8 days water stressed plants sampled 75 days after emergence. Treatment temperature was 53.5 C for 15 minutes.



EXPERIMENT 2

This study was designed to look at the effects of various combinations of heat and desiccation on the degree of injury to leaf tissue as measured by the conductivity method.

Preliminary Tests

Results of the preliminary tests are presented in Tables 25a through 25d. Significant increases in % injury were observed both with increase in heat and with increasing desiccation (Table 25a).

There was significantly more injury when leaf discs were taken from the uppermost fully expanded leaf than when they were taken from the third or the fourth uppermost fully expanded leaf (Table 25b). Leaf discs for further tests were therefore taken from the third and fourth uppermost fully expanded leaves with as uniform a mixture of leaf discs from the two leaves as was possible.

Though the differences were not statistically significant there was more injury when leaf discs were heated without water than when heated with 20 ml of water in the tube and when the holding period was 40 hours than when it was 18 hours (Tables 25c and 25d). The lack of statistical significance was likely due to insufficient replication.

The percent injury due to various combinations of heat and desiccation on leaf discs of two sorghum genotypes is

Table 25a. Effect of heating at various temperatures or desiccation with various concentrations of PEG 600 on percentage injury to leaf discs of three sorghum genotypes taken 65 days after emergence.

Genotype	Replication	Temperature (C) 48	50	52	54	55
		Percent Injury				
B	1	7.8	12.4	19.9	31.6	77.3
	2	7.6	15.9	9.2	80.0	77.1
	mean	7.7c[1]	14.2bc	14.6bc	55.8ab	77.2a
Martin B	1	5.7	15.2	15.6	---	---
	2	8.9	10.0	9.4	---	---
	mean	7.3a	12.6a	12.5a	---	---
226	1	6.8	16.9	9.1	---	---
	2	6.7	9.0	16.1	---	---
	mean	6.8a	13.0a	12.6a	---	---

Genotype	Replication	Concentration of PEG 600 in Water (%) 10 (-6.5 bars)	15 (-10 bars)	20 (-16 bars)
		Percent Injury		
B	1	0.3	2.6	20.3
	2	0.0	10.7	27.0
	3	1.1	2.9	28.0
	mean	0.5b	5.4b	25.1a

[1] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test.

Table 25b. Effect of leaf position on percentage injury to leaf discs of sorghum genotype 226 taken 67 days after emergence and heated at 53.5 C.

Replication	Leaf Position[1] 1	2	3	4
	Percent Injury			
1	91.1	88.1	83.3	84.5
2	91.5	94.0	86.7	84.6
mean	91.3a[2]	91.1ab	85.0bc	84.6bc

[1] Leaf 1 is the uppermost fully expanded leaf.

[2] Means followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test.

Table 25c. Effect of heating with and without water and the length of the holding period in the cold room on percentage injury to leaf discs of sorghum genotype 226 taken 70 days after emergence and heated at 51 C.

Water (ml)	Replication	Holding Period (hours) 18	40
		--------Percent Injury-------	
0	1	20.1	32.9
	2	15.8	52.8
	mean	18.0	42.9
20	1	35.4	55.7
	2	26.5	67.2
	mean	31.0	61.5

Table 25d. Effect of heating temperature and the length of the holding period in the cold room on percentage injury to leaf discs of sorghum genotype Martin B taken 76 days after emergence.

Temperature(C)	Replication	Holding Period (hours) 18	40
		-------Percent Injury-------	
48	1	6.5	9.9
	2	7.0	10.1
	mean	6.8	10.0
51	1	8.5	14.4
	2	13.9	26.3
	mean	11.2	20.4

presented in Table 26. Since the tests on genotypes B and Martin-B were conducted on separate occasions no attempt will be made to compare the responses of the two genotypes.

Genotype B (Martin x SC33-9-2-2-2)

In this genotype there appears to be no significant difference in the % injury caused due to heat or desiccation being applied first or both being applied together (compare treatments 5, 6 and 7; 8, 9 and 10; 11, 12 and 13; or 14, 15 and 16). A combination of mild heat and mild desiccation caused about as much injury as mild heat alone when heat followed or was applied with desiccation (1 vs 6 or 7). When mild heat preceeded mild desiccation the injury caused was closer to the sum of the injury caused by the two individual treatments (1 and 3 vs 5). A combination of mild heat and severe desiccation caused slightly more injury than the sum of the injury caused by the individual treatments irrespective of whether heat preceeded, followed or was applied with desiccation (1 and 4 vs 8, 9 and 10). Mild desiccation and severe heat caused no more injury than that caused by severe heat alone, regardless of how the two treatments were combined (2 and 3 vs 11, 12 and 13). The injury caused by a combination of severe heat and severe desiccation was about equal to the sum of the injury caused when the two treatments were individually applied (2 and 4 vs 14, 15 and 16).

Mild heat and mild desiccation in any combination caused

Table 26. Effect of various combinations of heat and desiccation treatments on percent injury to leaf discs of sorghum genotypes B and Martin B taken 72 and 76 days after emergence, respectively.

Treatment		Genotype	
		B	Martin B
		---%Injury---	
1	Heat treated at 48 C.	15.8de[1]	10.0d
2	Heat treated at 51 C.	38.5c	20.4d
3	Desiccated at -10 bars with PEG.	5.6e	9.5d
4	Desiccated at -23 bars with PEG.	39.6c	59.5b
5	Heat treated at 48 C then desiccated at -10 bars with PEG.	20.6de	---
6	Desiccated at -10 bars with PEG then heat treated at 48 C.	15.2de	---
7	Heat treated at 48 C while being desiccated at -10 bars with PEG.	14.7e	---
8	Heat treated at 48 C then desiccated at -23 bars with PEG.	59.5b	56.3b+
9	Desiccated at -23 bars with PEG then heat treated at 48 C.	60.1b	78.3a+
10	Heat treated at 48 C while being desiccated at -23 bars with PEG.	63.3ab	82.0a+
11	Heat treated at 51 C then desiccated at -10 bars with PEG.	31.4cd	38.0c+
12	Desiccated at -10 bars with PEG then heat treated at 51 C.	38.5c	63.2b+
13	Heat treated at 51 C while being desiccated at -10 bars with PEG.	39.0c	66.3b+
14	Heat treated at 51 C then desiccated at -23 bars with PEG.	76.7a	---
15	Desiccated at -23 bars with PEG then heat treated at 51 C.	76.5a	---
16	Heat treated at 51 C while being desiccated at -23 bars with PEG.	76.6a	---

[1] Means in the same column followed by the same letter(s) are not significantly different at $p = .05$ by Duncan's New Multiple Range Test.

about the same amount of injury as that caused by mild heat alone, which happened to be the most injurious of the two treatments in this particular test. Mild heat caused an increase in the injury caused by severe desiccation but mild desiccation did not increase the injury due to severe heat. When both stresses were severe the injury caused by a combination of the two stresses tended to be additive.

Genotype Martin-B

Only combinations of mild heat and severe desiccation or mild desiccation and severe heat were tested on this genotype (Table 26). The response to these treatments were different from those observed for genotype B above.

When mild heat preceeded severe desiccation the injury caused was about the same as that caused by severe desiccation alone (4 vs 8). When mild heat followed severe desiccation or when the two were applied together the resulting injury was appreciably more than the sum of that caused by the individual treatments (1 and 4 vs 9 and 10).

When severe heat preceeded mild desiccation the injury caused was slightly more than the sum of the injury caused by the individual treatments (2 and 3 vs 11). When severe heat followed mild desiccation or when the two were applied together the resulting injury was more than two times the sum of the injury caused by the individual treatments.

Thus, in this genotype mild heat increased the injury

due to severe desiccation except when the heat preceeded such desiccation, and mild desiccation increased the injury caused by severe heat but this increase was greater when the heat treatment followed desiccation or when the two stresses were applied together than when heat came first.

EXPERIMENT 3

Ten-day averages of maximum, minimum and weighted average temperatures are given in Table 27. Because of the late planting date temperatures gradually declined from emergence in environment 1 and from 30 days after emergence in environment 3.

Averages of periodic measurements of % relative humidity is plotted against time of day in Figure 13. In the morning (between 07 and 0800 hrs Central Standard Time) % relative humidity was the same at about 80% in both environments. Percent relative humidity declined with time of day to between 60 and 65% in environment 1 (cool) and to between 55 and 60% in environment 3 (hot) at about 1200 hrs CST. It stayed within these ranges for most of the remaining daylight hours and then began to rise at about 1900 hours. An average of about 5% difference in relative humidity between the two environments existed for most of this period.

Leaf Emergence Rate

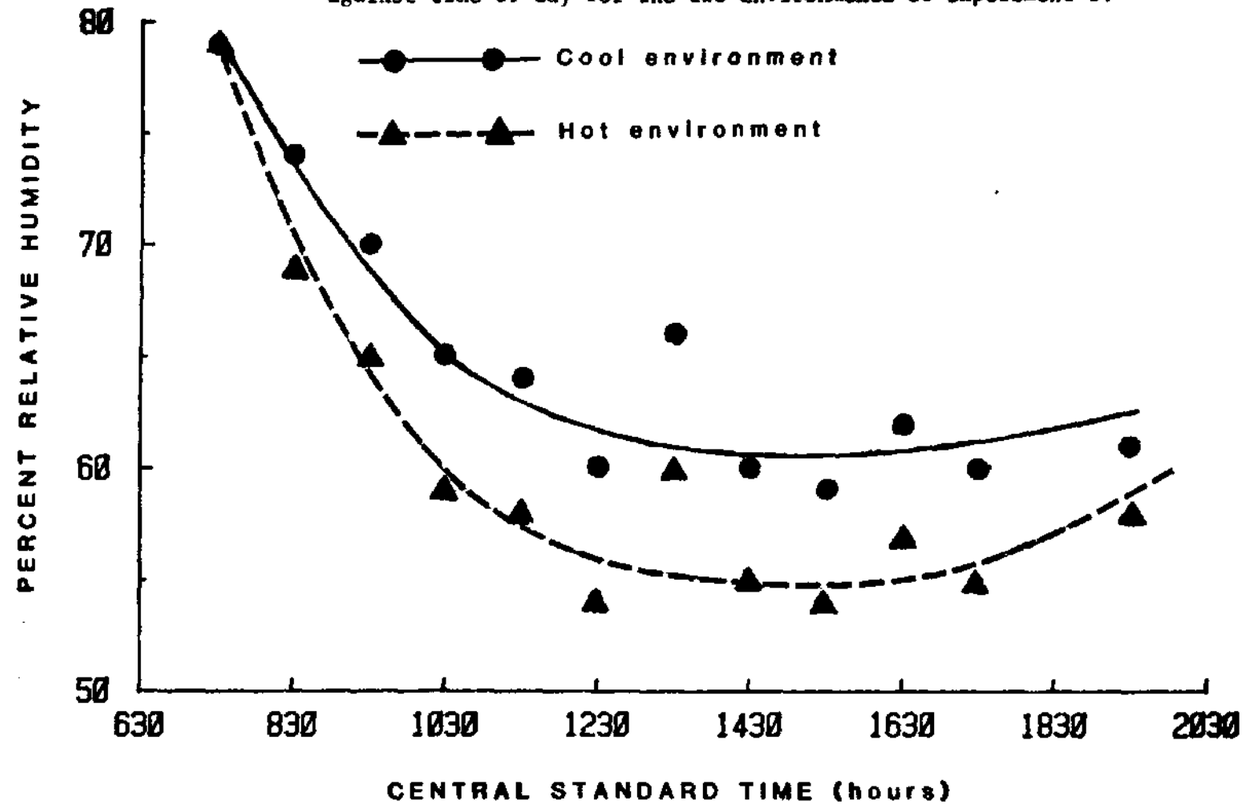
Rates of leaf emergence were recorded between 19 and 37 days after emergence before water stress was imposed. Only the effects of temperature and genotype on leaf emergence rates were therefore examined.

Unlike in experiment 1 where rate of leaf emergence was faster in the cool environment leaf emergence rates under the conditions of this experiment were slightly faster

Table 27. Ten-day averages of maximum, minimum and weighted average temperatures (C) for the two environments in experiment 3.

Days after emergence	ENVIRONMENT 1 (Cool)			ENVIRONMENT 3 (Hot)		
	Average maximum	Average minimum	Weighted average	Average maximum	Average minimum	Weighted average
	Temperature (C)					
0-10	35.0	18.6	25.7	37.9	22.0	28.3
11-20	31.2	17.7	23.6	35.4	23.4	28.1
21-30	30.9	16.5	22.6	40.1	24.0	29.7
31-40	29.3	17.5	22.3	37.2	23.6	28.5
41-50	27.8	16.1	21.0	36.6	21.7	27.1
51-60	26.3	16.1	20.6	34.8	19.5	25.4
61-70	25.6	15.0	19.5	33.3	18.1	24.0
71-80	24.3	12.9	17.8	34.2	16.1	23.2
81-90	24.2	12.1	17.5	32.7	15.7	22.8
91-100	23.6	11.3	16.9	31.8	14.6	21.9
101-110	25.3	7.8	14.5	29.8	11.2	18.5
Mean	27.6	14.7	20.2	34.9	19.1	25.2

Figure 13. Averages of periodic measurements of percent relative humidity plotted against time of day for the two environments of experiment 3.



in the hot environment for all three genotypes (Table 28). During the period of leaf growth the maximum, minimum and weighted average temperatures for the cool environment were fairly similar in experiment 1 and in this study, but both the minimum and weighted average temperatures for the hot environment were higher in this study than they were in experiment 1 (compare Tables 6 and 27). One possible explanation for the discrepancy in leaf emergence rates between the two studies could be the night temperatures. In experiment 1 the mean minimum temperatures were consistently higher by 0.5 to 1.2 C in the cool than in the hot environment (Table 6). In this study the mean minimum temperatures in the hot environment were 6 to 7 C higher than in the cool environment during the period of leaf development (Table 27). Any reductions in leaf growth due to elevated day temperatures in this study might have been compensated for by growth in the night, while in experiment 1 the night temperatures in the hot environment might have been too low to induce such compensatory growth.

As in experiment 1 genotype B had the slowest leaf emergence rate in both environments but genotypic differences were very small especially in environment 3 (Table 28).

Reproductive Development

Days to half-bloom and to physiological maturity are presented in Tables 29 and 29a respectively. The first

Table 28. Average number of fully expanded leaves on various days after emergence for three sorghum hybrids grown under two temperature environments.

Environment	Days after emergence	Genotype A	Genotype B	Genotype RS 626	Mean
		Number of Leaves			
1 (Cool)	19	5.2	5.0	5.2	5.1
	21	5.8	5.7	6.1	5.9
	26	7.5	6.9	7.4	7.3
	28	7.9	7.6	8.0	7.8
	30	8.7	8.2	8.7	8.5
	33	9.7	9.3	9.6	9.5
	37	10.9	10.4	11.1	10.8
3 (Hot)	19	5.1	5.1	5.3	5.2
	21	5.9	5.9	5.9	5.9
	26	7.7	7.4	7.7	7.6
	28	8.1	7.9	8.1	8.0
	30	8.9	8.8	8.8	8.8
	33	9.8	9.6	9.8	9.7
	37	11.1	10.9	11.3	11.1

increment of water stress (osmotically controlled with PEG) was not applied until 66 and 70 days after emergence, in the cool and hot environments, respectively. The slight differences in days to half-bloom in Table 29 were therefore not due to the water stress treatments. Elevated temperatures hastened flowering in all three genotypes. Genotype B flowered 3 to 5 days later than genotypes A and RS 626 in both environments. Genotype RS 626 flowered earlier than genotype A by 2 days in environment 1 and by a day in environment 3.

Physiological maturity was also hastened by elevated temperatures by an average of about 9 days. Days to physiological maturity was only slightly hastened by both low (-4 bars) and high (-6 bars) water stress in environment 1. In environment 3, -4 bars of water stress slightly hastened physiological maturity and -6 bars of water stress hastened it by about 3 days.

Yield and Yield Components

Panicle Weight

Weight of panicles is presented in Table 30. Except for genotype A in environment 3 plants that were subjected to -4 bars of water stress had heavier panicles than either the controls or those subjected to -6 bars of water stress in both environments. The differences between water stress treatments was significant in environment 1 but not in environment 3. Under non-water stressed (control) conditions

Table 29. Number of days from emergence to half bloom for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress(bars)	Genotype A	B	RS 626	Mean
		----------Number of Days----------			
	0	69.0	70.3	66.0	68.4
1	-4	68.0	71.5	65.8	68.4
(Cool)	-6	67.2	70.5	66.5	
	mean	68.1	70.8	66.1	
	0	64.0	67.5	63.3	64.9
3	-4	64.2	66.8	62.7	64.6
(Hot)	-6	63.2	66.2	62.8	64.1
	mean	63.8	66.8	62.9	

Table 29a. Number of days from emergence to physiological maturity for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress(bars)	Genotype A	B	RS 626	Mean
		----------Number of Days----------			
	0	102.3	107.7	102.3	104.1
1	-4	100.7	109.5	100.2	103.4
(Cool)	-6	99.3	109.3	101.2	103.3
	mean	100.8	108.8	101.2	
	0	93.0	100.0	93.7	95.6
3	-4	92.8	99.0	93.0	94.9
(Hot)	-6	90.7	97.3	90.2	92.7
	mean	92.2	98.8	92.3	

genotype A produced about the same size panicles in the two environments, genotype B had heavier panicles in environment 3 and genotype RS 626 had heavier panicles in environment 1. Under low water stress all three genotypes had heavier panicles in environment 1 than in environment 3. Under high water stress genotype A had heavier panicles in environment 3 but genotypes B and RS 626 had heavier panicles in environment 1. Genotype B had significantly heavier panicles than the two other genotypes in both environments. On the average panicles were heavier in environment 1 than in environment 3 but the difference was not significant (Table 30).

Number of Seeds

Table 31 gives seed numbers in grams per plant and as percentages of the first treatment combination (genotype A, water stress 0, environment 1). Water stress did not significantly affect seed numbers in either environment. This was likely due to the mildness of the stress and the stage of growth at which it was imposed. Bennett (1979) also reported that -7.5 bars of water stress applied at bloom significantly reduced seed numbers in only one of four sorghum hybrids tested.

In environment 1 genotype RS 626 had significantly greater seed numbers than genotypes A and B but there were no significant genotypic differences in environment 3. The difference in seed numbers between the two environments was also not significant (Table 31).

Table 30. Panicle weight (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Panicle Weight			
1 (Cool)	0	44.7 (100)d[1,2]	58.8 (132)abc	59.0 (132)abc	54.1 (121)b[3]
	-4	62.0 (139)ab	67.0 (150)a	61.1 (137)ab	63.4 (142)a
	-6	49.6 (111)bcd	56.9 (127)abcd	46.3 (104)cd	50.9 (114)b
	mean	52.1 (117)b[4]	60.9 (136)a	55.4 (124)ab	
3 (Hot)	0	45.6 (102)bc	63.1 (141)a	55.0 (123)abc	54.6 (122)a
	-4	48.6 (109)abc	63.3 (142)a	59.9 (134)ab	57.3 (128)a
	-6	56.1 (126)abc	55.1 (123)abc	41.0 (92)c	50.7 (113)a
	mean	50.1 (112)b	60.5 (135)a	52.0 (116)b	

Overall Means

Environment	Panicle weight	Water stress	Panicle weight	Genotype	Panicle weight
1	56.1 (126)a[3]	0	54.4 (122)b	A	51.1 (115)b
3	54.2 (121)a	-4	60.3 (135)a	B	60.7 (136)a
		-6	50.8 (114)b	RS 626	53.7 (120)b

[1] Numbers in parentheses are panicle weights expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 31. Number of seeds per plant for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Number of Seeds			
1 (Cool)	0	1719 (100)c[1,2]	1932 (132)abc	2239 (130)ab	1963 (114)a[3]
	-4	2144 (125)abc	1956 (114)abc	2288 (133)a	2129 (124)a
	-6	1825 (106)bc	1924 (112)abc	2240 (130)ab	1996 (116)a
	mean	1896 (110)b[4]	1937 (113)b	2256 (131)a	
3 (Hot)	0	1845 (107)b	2193 (128)ab	2083 (121)ab	2040 (119)a
	-4	1900 (111)b	2152 (125)ab	2256 (131)ab	2103 (122)a
	-6	2496 (145)a	1998 (116)ab	1931 (112)b	2141 (125)a
	mean	2080 (121)a	2114 (123)a	2090 (122)a	

Overall Means

Environment	Seed number	Water stress	Seed number	Genotype	Seed number
1	2030 (118)a[3]	0	2002 (116)a	A	1998 (116)b
3	2095 (122)a	-4	2116 (123)a	B	2026 (118)ab
		-6	2069 (120)a	RS 626	2173 (126)a

[1] Numbers in parentheses sre seed numbers expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Seed Size

Weight of 1000 seeds was highest under low (-4 bars) water stress in both environments but the difference between control (non-water stressed) and low water stress was not significant in either environment (Table 32). This may have been because of greater assimilates being available for translocation to the grains under mild stress than under control conditions. Water stress of about -4 bars has been found to increase photosynthetic rates of some sorghum genotypes over controls (C. Y. Sullivan, Personal communication). The difference between low water stress and controls became significant when averaged over environments (Table 32).

Genotype B had significantly heavier seeds than genotypes A and RS 626. This was partly because it had a grain filling period of 3 to 5 days longer than both genotypes in both environments (Tables 29 and 29a).

Unlike in experiment 1 where seed size was greater in environment 3 than in environment 1 seeds were significantly heavier in environment 1 in this study. This is again because the water stress levels in this study were not as severe as they were in experiment 1 where seed numbers in environment 3 were drastically reduced with increasing water stress. Furthermore, the length of the grain filling period was an average of 6 to 7 days longer in environment 1 than in environment 3 (see Tables 29 and 29a).

Table 32. Weight of 1000 seeds (g) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Weight of 1000 Seeds			
1 (Cool)	0	17.9 (100)c[1,2]	22.3 (125)ab	19.0 (106)bc	19.7 (110)ab[3]
	-4	20.8 (116)bc	25.8 (144)a	19.1 (107)bc	21.9 (122)a
	-6	19.7 (110)bc	21.8 (122)bc	13.3 (74)d	18.3 (102)b
	mean	19.4 (108)b[4]	23.3 (130)a	17.1 (96)c	
3 (Hot)	0	16.6 (93)cd	19.9 (111)ab	18.9 (106)abc	18.4 (103)a
	-4	17.8 (99)bcd	21.5 (120)a	19.2 (107)abc	19.5 (109)a
	-6	15.6 (87)d	18.9 (106)abc	15.2 (85)d	16.5 (92)b
	mean	16.6 (93)b	20.1 (112)a	17.7 (99)b	

Overall Means

Environment	1000-seed weight	Water stress	1000-seed weight	Genotype	1000-seed weight
1	20.0 (112)a[3]	0	19.1 (107)b	A	18.0 (101)b
3	18.1 (101)b	-4	20.7 (116)a	B	21.7 (121)a
		-6	17.4 (97)c	RS 626	17.4 (97)b

[1] Numbers in parentheses are seed weights expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Grain Yield

Following the trend in seed numbers and seed size the highest grain yield in both environments was obtained under low (-4 bars) water stress (Table 33). Average grain yield was slightly higher under control (non-water stressed) conditions than under high (-6 bars) water stress but the difference was not significant (Table 33).

Genotype B had significantly higher grain yield than genotypes A and RS 626 in both environments.

Average grain yield was higher in environment 1 than in environment 3 but the difference was not significant (Table 33).

Other Plant Parts

As with the grain yield, leaf and stem dry matter in both environments were highest under low (-4 bars) water stress but they were not significantly different from the controls (Tables 34 and 35). Leaf and stem dry matter were higher in genotype A than in genotypes B and RS 626 in both environments. This was mainly because genotype A tillered more profusely than the other genotypes in both environments. There were no differences in leaf weight between the two environments but stem dry matter was significantly higher in environment 1. This was despite more tillering by all genotypes in environment 3.

Root dry matter is presented in Table 36. In environment 1 water stress had no effect on root weights in genotypes

Table 33. Grain yield (g per plant) for three sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Grain Yield			
1 (Cool)	0	30.5 (100)c[1,2]	42.2 (138)abc	41.7 (137)abc	38.1 (125)b[3]
	-4	44.3 (145)ab	49.4 (162)a	44.4 (146)ab	46.0 (151)a
	-6	35.6 (117)bc	41.7 (137)abc	30.5 (100)c	36.0 (118)b
	mean	36.8 (121)b[4]	44.4 (146)a	38.9 (128)ab	
3 (Hot)	0	30.8 (101)c	43.7 (143)ab	39.2 (129)abc	37.9 (124)ab
	-4	34.1 (112)bc	46.2 (151)a	43.3 (142)ab	41.2 (135)a
	-6	39.0 (128)abc	38.3 (126)abc	28.0 (92)c	35.1 (115)b
	mean	34.6 (113)b	42.7 (140)a	36.8 (121)b	

Overall Means

Environment	Grain yield	Water stress	Grain yield	Genotype	Grain yield
1	40.0 (131)a[3]	0	38.0 (125)b	A	35.7 (117)b
3	38.1 (125)a	-4	43.6 (143)a	B	43.6 (143)a
		-6	35.5 (116)b	RS 626	37.8 (124)b

[1] Numbers in parentheses are grain yields expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 34. Leaf dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Leaf Dry Matter			
1 (Cool)	0	24.7 (100)ab[1,2]	21.3 (86)abcd	17.5 (71)cd	21.2 (86)ab[3]
	-4	26.1 (106)a	20.3 (82)bcd	20.7 (84)abcd	22.4 (91)a
	-6	22.8 (92)abc	21.7 (88)abcd	16.6 (67)d	20.4 (83)b
	mean	24.5 (99)a[4]	21.1 (85)b	18.3 (74)b	
3 (Hot)	0	26.6 (108)a	21.9 (89)bc	16.8 (68)d	21.8 (88)a
	-4	23.8 (96)abc	22.9 (93)abc	19.7 (80)cd	22.1 (89)a
	-6	24.9 (101)ab	20.1 (81)cd	16.4 (66)d	20.5 (83)a
	mean	25.1 (102)a	21.7 (88)b	17.6 (71)c	

Overall Means

Environment	Leaf dry matter	Water stress	Leaf dry matter	Genotype	Leaf dry matter
1	21.3 (86)a[3]	0	21.5 (87)ab	A	24.8 (100)a
3	21.5 (87)a	-4	22.3 (90)a	B	21.4 (87)b
		-6	20.4 (83)b	RS 626	17.9 (72)c

[1] Numbers in parentheses are leaf dry matter expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 35. Stem dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress(bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Stem Dry Matter			
1 (Cool)	0	45.8 (100)ab[1,2]	43.0 (94)ab	40.2 (88)bc	43.0 (94)a[3]
	-4	53.3 (116)a	39.9 (87)bc	40.8 (89)bc	44.6 (97)a
	-6	43.1 (94)ab	36.8 (80)bc	30.3 (66)c	36.7 (80)b
	mean	47.4 (103)a[4]	39.9 (87)b	37.1 (81)b	
3 (Hot)	0	44.6 (97)a	38.9 (85)a	34.3 (75)ab	39.3 (86)a
	-4	42.3 (92)a	42.8 (93)a	36.8 (80)ab	40.6 (89)a
	-6	41.5 (91)a	34.3 (75)ab	26.8 (59)b	34.2 (75)b
	mean	42.8 (93)a	38.6 (84)a	32.7 (71)b	

Overall Means

Environment	Stem dry matter	Water stress	Stem dry matter	Genotype	Stem dry matter
1	41.5 (91)a[3]	0	41.1 (90)a	A	45.1 (98)a
3	38.0 (83)b	-4	42.6 (93)a	B	39.3 (86)b
		-6	35.4 (77)b	RS 626	34.9 (76)c

[1] Numbers in parentheses are stem dry matter expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR)

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 36. Root dry matter (g per plant) for 3 sorghum hybrids grown under two temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype A	Genotype B	Genotype RS 626	Mean
		Root Dry Matter			
1 (Cool)	0	26.2 (100)a[1,2]	22.3 (85)a	21.8 (83)a	23.4 (89)a[3]
	-4	26.2 (100)a	22.3 (85)a	20.8 (79)a	23.1 (88)a
	-6	26.2 (100)a	22.0 (84)a	13.6 (52)b	20.6 (79)a
	mean	26.2 (100)a[4]	22.2 (85)b	18.8 (72)c	
3 (Hot)	0	27.7 (106)abc	26.0 (99)abc	20.8 (79)c	24.8 (95)a
	-4	30.6 (117)a	28.1 (107)ab	22.9 (87)bc	27.2 (104)a
	-6	27.4 (105)abc	21.4 (82)bc	14.5 (55)d	21.1 (81)b
	mean	28.6 (109)a	25.2 (96)a	19.4 (74)b	

Overall Means

Environment	Root dry matter	Water stress	Root dry matter	Genotype	Root dry matter
1	22.4 (85)a[3]	0	24.1 (92)a	A	27.4 (105)a
3	24.4 (93)a	-4	25.1 (96)a	B	23.7 (90)b
		-6	20.8 (79)b	RS 626	19.1 (73)c

[1] Numbers in parentheses are root dry matter expressed as percentages of genotype A, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

A and B but root weight in RS 626 was drastically reduced by high (-6 bars) water stress. In environment 3 low water stress caused a slight increase in root weight over controls for all three genotypes. High water stress had again no effect on root weight in genotype A but root weight in genotype B was reduced by 18% and in RS 626 by 30%. There were significant genotypic differences in root weight in both environments. Genotype A had the greatest root weight and RS 626 the least root weight in both environments.

Average root weight was higher in environment 3 than in environment 1 though the difference was not significant. This trend was also observed in experiment 4. While elevated temperatures reduced above ground growth it had no apparent effect on root growth. Though the temperature of the root environment may not have been as high as that of the air temperature there was likely to be some difference between the hot and the cool environments.

Interactions of Water Stress and Temperature

Water stress by environment interactions were not significant for any of the plant parameters measured in this study. This may be because the water stress levels in this study were quite mild, as such interactions were observed in experiment 1.

EXPERIMENT 4

This experiment was designed to look at water use by plants in two temperature environments. Consumptive water use was measured for a four-week period from 4 days after emergence until plants were harvested at 32 days after emergence. Temperature recording started 8 days after emergence. During the 25-day period for which temperatures were recorded the weighted average daily temperatures were 23.7 C in the cool environment and 28 C in the hot environment.

Leaf 5 (counting the first small rounded leaf as leaf 1) being close to the middle of the shoot axis was considered to be a representative leaf and was selected for estimate of leaf area. Area of leaf 5 was estimated by the regression of leaf area on the product of leaf length and leaf width. Various authors have reported a range of factors for converting the product of leaf length and width of sorghum to leaf area. Stickler et al. (1961) reported a factor of .747 for six sorghum genotypes; Krishnamurthy et al. (1974) reported .71 for three sorghum genotypes; Bishnoi (1966) .795 for sweet sorghums and .689 for non-sweet sorghums; and McCree and Davies (1974) using regression method reported a factor of .685 and stated that this factor was not affected by water stress or temperature. The regression equations obtained in this study did not vary very much among the three genotypes examined (Table 37). When the formula Leaf Area/(Length X Width)

Table 37. Regression equations and estimates of leaf area from the product of leaf length and leaf width for three sorghum hybrids.

Genotype	Regression equation	r^2	$S_{y.x}$	n
A	Y = 0.7565X - 4.868	0.9972	21.49	45
B	Y = 0.7642X - 6.941	0.9956	36.44	40
RS 626	Y = 0.7630X - 6.290	0.9937	44.52	51

X (L x W)	Y (Estimated leaf area, cm^2) Genotype A	B	RS 626
20	10.3	8.3	9.0
40	25.4	23.6	24.2
80	55.7	54.2	54.8
120	85.9	84.8	85.3
160	116.2	115.3	115.8
200	146.4	145.9	146.3
240	176.7	176.5	176.8
280	207.0	207.0	207.4
320	237.2	237.6	237.9
360	267.5	268.2	268.4
400	297.7	298.7	298.9
440	328.0	329.3	329.4

was used it was noticed that the factor increased from an average of .49 for the second leaf to about .76 for the 11th leaf and then declined (Table 37a). The regression equation thus gives a much better estimate of canopy leaf area than a factor derived from average leaf area, average leaf length and width, though the regression equations do grossly underestimate the areas of the 2nd and 3rd leaves. When estimating canopy leaf area however, these leaves contribute so little to the total leaf area that the error can be neglected.

Genotype B had significantly larger area for leaf 5 than both genotypes A and RS 626 in both environments but the difference between the two environments was not significant (Table 38).

There were also small but significant genotypic differences in the weight of roots and shoots and total dry matter in both environments.

Genotype RS 626 used the greatest amount of water in both environments. Genotype B used more water than genotype A in environment 1 but genotype A used more in environment 3. When water use was converted to ml of water used per g of total plant dry matter produced genotype B used the most in both environments and was thus the least efficient, but genotypic differences were significant only in environment 1 and when averaged over environments (Table 38).

Though the difference in total water used between the

Table 37a. Ratio of actual leaf area to the product of leaf length and width for three sorghum hybrids.

Leaf number	Genotype			Mean
	A	B	RS 626	
	Ratio			
2	.417	.585	.480	.494
3	.517	.542	.498	.519
4	.553	.680	.571	.601
5	.648	.667	.672	.662
6	.680	.679	.682	.680
7	.690	.697	.705	.697
8	.693	.694	.702	**.696**
9	.711	.690	.687	.696
10	.716	.728	.693	.712
11	.781	.736	.772	.763
12	.753	.763	.737	.751
13	.744	.740	.725	.736
14	.734	.741	.747	.741
15	.728	--	.797	.763
16	.738	--	.737	.738
17	--	--	.714	.714

Table 38. Dry matter, water use efficiency, and area of leaf 5 for three sorghum hybrids grown under two temperature environments.

	Environment 1 (Cool)			Environment 3 (Hot)			Genotype means			Environment means	
	Genotype			Genotype							
	A	B	RS 626	A	B	RS 626	A	B	RS 626	1 (Cool)	3 (Hot)
Root dry matter (g/plant)	2.0b[1]	2.4a	2.5a	2.5b	2.3b	2.9a	2.3b	2.3b	2.7a	2.3a	2.6a
Shoot dry matter (g/plant)	11.4b	11.8b	14.6a	12.1b	9.8b	14.9a	11.8b	10.8b	14.7a	12.6a	12.3a
Total dry matter (g/plant)	13.5b	14.1b	17.1a	14.5b	12.2b	17.7a	14.0b	13.1b	17.4a	14.9a	14.8a
Total water use (ml/plant)	1110b	1378ab	1439a	1718a	1479b	1931a	1414b	1429b	1685a	1309a	1709a
WUE (g/ml)	82b	97a	86b	120a	124a	113a	101b	111a	99b	88b	119a
Area of 5th leaf (cm^2)	21.5b	37.8a	24.0b	22.5b	27.5a	21.4b	22.0b	32.6a	22.7b	27.8a	23.8a

[1] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test.

two environments was large (more than 30%) it was not significant. Efficiency of water use was however significantly higher in environment 1 (Less water used per g of dry matter produced). Most of the excess water use in environment 3 was likely due to increased evapotranspiration.

EXPERIMENT 5

Figure 14 shows the relative humidity (two upper curves) and temperature (two lower curves) plotted against time of day during one 24-hour period for the two controlled environmental chambers used in this experiment. The night temperatures remained constant at 22.5 C in both environments and the day temperatures of 30 C for the cooler environment and 40 C for the hot environment, were fairly well maintained.

During the daily 10-hour light period photosynthetically active radiation (PAR) averaged about 700 $\mu Em^{-2}sec^{-1}$.

Leaf Expansion

Regression equations for estimating leaf area from leaf length and leaf width were developed as reported in experiment 4. The regression equations for the three genotypes are presented in Table 39. Once again the factor derived from leaf area/(Leaf length x Leaf width) increased from leaf 2 until it reached a maximum at leaf 10 for genotype 121, and leaves 16 and 15 for 160 and RS 626, respectively, and then declined (Table 39a).

Leaves 5 and 6 were again chosen as representing typical leaves of the plant and their area estimated from the regression equations of Table 39. The estimated leaf area is presented in Table 40. It is important to note that in the case of environments 2 (transferred from hot to cool) and 4 (transferred from cool to hot) these two leaves were expanded after

Figure 14. Relative humidity (%) and temperature (C) in the two controlled environmental chambers of experiment 5 during one 24-hour period.

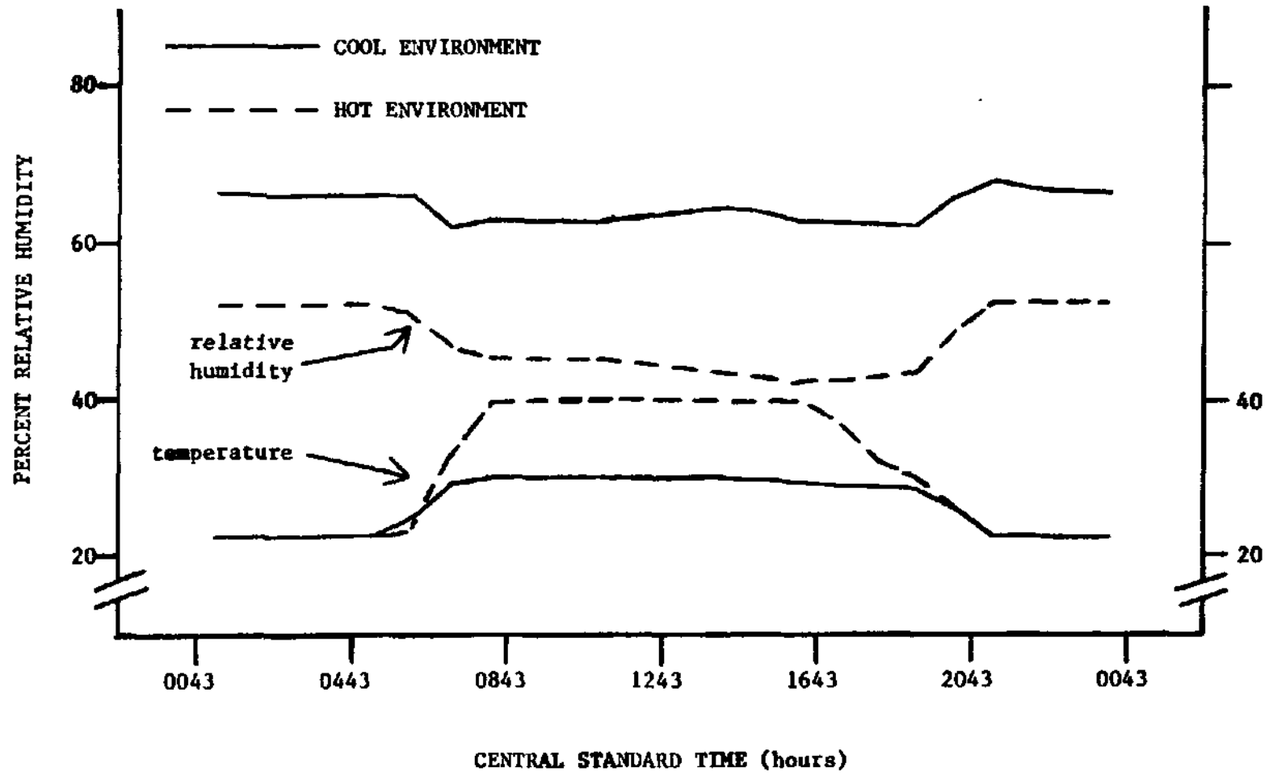


Table 39. Regression equations developed from measurements of leaf length, leaf width, and actual leaf area for three sorghum genotypes.

Genotype	Regression equation	R^2	$S_{y \cdot x}$	n
121	Y = 0.745X - 6.555	0.998	14.77	36
160	Y = 0.773X - 5.078	0.994	44.92	51
RS 626	Y = 0.763X - 6.290	0.994	44.52	51

X	Genotype		
(L x W)	121	160	RS 626
	Estimated Leaf Area		
20	8.4	10.4	9.0
80	53.1	56.8	54.8
160	112.7	118.6	115.8
240	172.3	180.4	176.8
320	231.9	242.2	237.9
400	291.5	304.1	298.9

Table 39a. Ratio of actual leaf area to the product of leaf length and leaf width for various leaves of three sorghum genotypes.

Leaf	Genotype			
Number	121	160	RS 626	Mean
	Ratio			
2	.460	.417	.480	.452
3	.494	.477	.498	.490
4	.557	.551	.571	.560
5	.635	.637	.672	.648
6	.644	.670	.682	.665
7	.687	.700	.705	.697
8	.690	.716	.702	.703
9	.695	.712	.687	.698
10	.747	.714	.693	.718
11	.729	.749	.772	.750
12	.718	.775	.737	.747
13	—	.770	.725	.748
14	--	.722	.747	.735
15	--	.756	.797	.778
16	--	.804	.737	.771
17	--	.755	.714	.735
18	--	.701	.714	.708

the plants were transferred.

Both -3 and -4.5 bars of water stress significantly reduced the area of the fully expanded leaves of all genotypes from those of the controls in environments 1 (cool) and 3 (hot), and leaf area under -4.5 bars of water stress was significantly smaller than leaf area under -3 bars of water stress in both environments (Table 40). No controls were included with plants that were transferred from the hot to the cool environment (environment 2) and from the cool to the hot environment (environment 4) mid-way through the water stress treatments. In these two environments the differences in leaf area between -3 and -4.5 bars of water stress were not significant for any of the three genotypes.

Leaf area in environment 1 was significantly larger than in environment 3 for all three genotypes and under all water stress levels, and the difference was greater under control (non-water stressed) conditions than under either -3 or -4.5 bars of water stress. Thus both elevated temperatures and water stress reduced leaf area independently and in combination.

For the two leaves measured, genotypes 121 and RS 626 had significantly greater leaf area than genotype 160. This may not reflect differences in total leaf area as genotype 160 was generally one fully expanded leaf ahead of the two other genotypes.

When averaged over genotypes and water stress treatments the differences in leaf area between the four environments

Table 40. Area of leaves 5 and 6 (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	Genotype 160	Genotype RS 626	Mean
		Leaf Area			
1	0	119 (100)a[1,2]	104 (87)ab	117 (98)a	113 (95)a[3]
	-3	90 (76)b	69 (58)cd	94 (79)b	84 (71)b
	-4.5	74 (62)c	53 (45)d	69 (58)cd	65 (55)c
	mean	94 (79)a[4]	75 (63)b	94 (79)a	
2	-3	94 (79)ab	77 (65)b	96 (81)ab	89 (75)a
	-4.5	103 (87)a	76 (64)b	76 (64)b	85 (71)a
	mean	98 (82)a	76 (64)b	86 (72)ab	
3	0	97 (82)a	92 (77)a	105 (88)a	98 (82)a
	-3	86 (72)a	65 (55)b	87 (73)a	79 (66)b
	-4.5	59 (50)b	46 (39)b	50 (42)b	52 (44)c
	mean	80 (67)a	68 (57)b	81 (68)a	
4	-3	75 (63)ab	80 (67)ab	82 (69)ab	79 (66)a
	-4.5	75 (63)ab	61 (51)b	90 (76)a	75 (63)a
	mean	75 (63)ab	71 (60)b	86 (72)a	

Overall Means

Environment	Leaf area	Water stress	Leaf area	Genotype	Leaf area
1	88 (74)a[3]	0	106 (89)a	121	87 (73)a
2	87 (73)a	-3	83 (70)b	160	72 (61)b
3	76 (64)a	-4.5	69 (58)c	RS 626	87 (73)a
4	77 (65)a				

[1] Numbers in parentheses are leaf area expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

were not significant. Apart from the reduction in leaf dimensions leaf area in environments 3 and 4 were further reduced due to hastened leaf senescence even in the non-water stressed plants. After relief of water stress, plants that were stressed at -4.5 bars in environment 4 were smaller than all other plants but their leaves were greener and showed less drying than either the controls or those stressed at -3 bars.

Photosynthesis

Net photosynthetic rates measured 18 and 24 days after emergence (8 and 14 days after relief of water stress) are presented in Tables 41 and 41a, respectively.

In the first set of measurements (Table 41) differences in responses to water stress treatments were not significant in any of the environments, although average photosynthetic rates per unit leaf area in environments 1 and 3 were slightly higher in both -3 and -4.5 bars water stressed plants than in the controls (Table 41). Total photosynthesis was probably more in the controls because of the significantly larger leaf area (Table 40). When averaged over genotypes and water stress treatments photosynthetic rates were significantly higher in environment 1 than in environments 2, 3 or 4. Genotypic differences were also not significant for this first set of measurements (Table 41).

In the second set of measurements of photosynthetic rates

Table 41. Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 18 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	Genotype 160	Genotype RS 626	Mean
		Net Photosynthetic Rates			
1	0	34.6 (100)a[1,2]	53.8 (155)a	19.6 (57)a	36.0 (104)a[3]
	-3	48.1 (139)a	29.3 (85)a	42.2 (122)a	38.8 (112)a
	-4.5	40.4 (117)a	33.4 (97)a	54.1 (156)a	42.9 (124)a
	mean	40.1 (116)a[4]	38.8 (112)a	38.6 (112)a	
2	-3	39.2 (113)a	30.1 (87)a	29.9 (86)a	33.1 (96)a
	-4.5	21.4 (62)a	35.1 (101)a	23.6 (68)a	25.7 (74)a
	mean	30.3 (88)a	32.1 (93)a	26.8 (77)a	
3	0	26.6 (77)ab	30.8 (89)ab	19.7 (57)ab	25.7 (74)a
	-3	30.4 (88)ab	20.9 (60)ab	42.9 (124)ab	31.4 (91)a
	-4.5	9.2 (27)b	51.4 (149)a	46.0 (133)ab	34.2 (99)a
	mean	22.1 (64)a	34.3 (99)a	35.0 (101)a	
4	-3	34.8 (101)a	17.2 (50)a	43.4 (125)a	31.8 (92)a
	-4.5	20.7 (60)a	32.0 (92)a	42.7 (123)a	31.8 (92)a
	mean	27.8 (80)a	24.6 (71)a	43.1 (124)a	

Overall Means

Environment	PS rate	Water stress	PS rate	Genotype	PS rate
1	39.1 (113)a[3]	0	30.8 (89)a	121	29.6 (86)a
2	29.6 (86)b	-3	33.6 (97)a	160	33.3 (96)a
3	30.3 (88)b	-4.5	33.6 (97)a	RS 626	36.1 (104)a
4	31.8 (92)b				

[1] Numbers in parentheses are photosynthetic rates expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

(Table 41a) water stress treatment differences were significant in environment 3 and when averaged over environments. In environment 3 photosynthetic rates were significantly higher for plants that were water stressed at -4.5 bars than for the controls or those that were water stressed at -3 bars. This reflects the point about less injury to leaves of -4.5 bars water stressed plants in environment 3 mentioned above. This may reflect a certain degree of "hardening" or "acclimation" to elevated temperatures caused by their earlier simultaneous exposure to -4.5 bars of water stress and elevated temperatures. Such "hardening" was not observed in plants subjected to -4.5 bars of water stress in environment 4 where the plants were first subjected to water stress in the cool environment and then transferred to the hot environment (Table 41a). In fact photosynthetic rates were severely affected by this treatment when the first measurement (Table 41) was compared to the second measurement (Table 41a).

Plants that were subjected to elevated temperatures and then water stressed (environment 2) showed substantially higher photosynthetic rates than those that were water stressed before being subjected to elevated temperatures (environment 4). Average photosynthetic rates were higher in environments 1 and 2 than in environments 3 and 4 (Table 41a).

Genotype 121 had higher photosynthetic rates than genotypes 160 and RS 626 in environments 1, 2, and 3, but the differences were only significant under -4.5 bars of water

Table 41a. Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 24 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	Genotype 160	Genotype RS 626	Mean
		Net Photosynthetic Rates			
1	0	35.2 (100)a[1,2]	32.1 (91)a	33.0 (94)a	33.4 (95)a[3]
	-3	43.1 (122)a	32.3 (92)a	37.2 (106)a	37.5 (107)a
	-4.5	44.8 (127)a	33.6 (95)a	34.6 (98)a	37.6 (107)a
	mean	41.0 (116)a[4]	32.7 (93)a	34.9 (99)a	
2	-3	36.9 (105)a	25.1 (71)a	32.1 (91)a	31.5 (89)a
	-4.5	37.6 (107)a	29.2 (83)a	29.9 (85)a	32.3 (92)a
	mean	37.3 (106)a	27.5 (78)a	31.0 (88)a	
3	0	8.6 (24)b	9.2 (26)b	8.3 (24)b	8.7 (25)b
	-3	9.8 (28)b	4.6 (13)b	4.4 (13)b	6.3 (18)b
	-4.5	71.1 (202)a	30.0 (85)b	22.2 (63)b	41.1 (117)a
	mean	29.8 (85)a	14.6 (41)ab	11.6 (33)b	
4	-3	0.0 (0)a	14.6 (41)a	6.2 (18)a	7.8 (22)a
	-4.5	9.5 (27)a	7.4 (21)a	3.2 (9)a	6.7 (19)a
	mean	5.7 (16)a	11.0 (31)a	4.7 (13)a	

Overall Means

Environment	PS rate	Water stress	PS rate	Genotype	PS rate
1	36.2 (103)a[3]	0	21.1 (60)b	121	30.5 (87)a
2	31.9 (91)ab	-3	20.5 (58)b	160	21.7 (62)b
3	18.7 (53)ab	-4.5	29.4 (84)a	RS 626	21.1 (60)b
4	7.2 (20)b				

[1] Numbers in parentheses are photosynthetic rates expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

stress in environment 3, and when averaged over environments (Table 41a). In environment 4 genotype 160 had the highest photosynthetic rates under -3 bars of water stress but genotype 121 again had higher photosynthetic rates under -4.5 bars of water stress, but the differences were not significant.

Dry Matter Accumulation

Dry matter accumulation rates between 19 and 27 days after emergence (between 9 and 17 days after relief of water stress) is presented in Table 42. These rates were calculated from the dry weights in Appendix Tables A4 and A5.

In environment 1 (cool) dry matter accumulation rates declined with increase in water stress for all three genotypes. There were no genotypic differences in dry matter accumulation rates under control (non-water stressed) conditions but under -3 and -4.5 bars of water stress both RS 626 and 121 had significantly greater dry matter accumulation rates than genotype 160.

In environment 2 (transferred from hot to cool) -4.5 bars of water stress caused a slight increase in dry matter accumulation rates of all genotypes over those under -3 bars of water stress.

In environment 3 (hot) -3 bars of water stress resulted in a slight increase in the dry matter accumulation rates of genotypes 121 and RS 626 and a slight decline for genotype 160. Water stress of -4.5 bars caused no further decrease in the dry matter accumulation rates of genotype 160, but it

Table 42. Dry matter accumulation rates (mg per day) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Dry Matter Accumulation Rates			
1	0	290 (100)a[1,2]	282 (97)a	282 (97)a	285 (98)a[3]
	-3	243 (84)ab	169 (58)cd	249 (86)ab	220 (76)ab
	-4.5	190 (66)bcd	129 (44)d	201 (69)bc	173 (60)b
	mean	241 (83)a[4]	193 (67)b	244 (84)a	
2	-3	254 (88)a	162 (56)b	243 (84)a	220 (76)a
	-4.5	275 (95)a	200 (69)ab	252 (87)a	242 (83)a
	mean	265 (91)a	181 (62)b	248 (86)a	
3	0	149 (51)abc	103 (36)bc	185 (64)a	146 (50)a
	-3	169 (58)ab	88 (30)c	207 (71)a	155 (53)a
	-4.5	89 (31)c	87 (30)c	87 (30)c	87 (30)b
	mean	136 (47)a	92 (32)b	160 (55)a	
4	-3	129 (44)b	128 (44)b	251 (87)a	169 (58)a
	-4.5	119 (41)b	123 (42)b	170 (59)b	137 (47)a
	mean	124 (43)b	126 (43)b	211 (73)a	

Overall Means

Environment	Accum. rates	Water stress	Accum. rates	Genotype	Accum. rates
1	226 (78)a[3]	0	215 (74)a	121	191 (66)b
2	231 (80)a	-3	191 (66)ab	160	147 (51)c
3	129 (44)b	-4.5	160 (55)b	RS 626	213 (73)a
4	153 (53)ab				

1 Numbers in parentheses are dry matter accumulation rates expressed as percentages of genotype 121, water stress 0, environment 1.

2 Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

3 Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

4 Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

drastically reduced the accumulation rates of genotypes 121 and RS 626. Thus under cool temperatures genotype 160 was more sensitive to water stress but under high temperatures genotypes 121 and RS 626 were more sensitive to water stress (compare environments 1 and 3, Table 42).

In environment 4 (transferred from cool to hot) -4.5 bars of water stress resulted in a significant decrease in dry matter accumulation rates of genotype RS 626 but caused only minimal decreases in the two other genotypes.

Dry matter accumulation rates under all levels of water stress were higher in environment 1 than in environment 3. Differences between -3 and -4.5 bars of water stress were not significant in environments 2 and 4 but the rates under both water stress treatments were greater in environment 2 than in environment 4 (Table 42). Exposure to elevated temperatures following mild water stress (environment 4) seemed more deleterious to seedlings of all three genotypes than when such water stress was preceeded by exposure to elevated temperatures (environment 2, Table 42).

EXPERIMENT 6

Relative humidity (%) and temperature (C) averages over a typical five-day period are plotted against time of day in Figure 15. The night temperatures in both environments remained constant at 22 C and the day temperature in the cool environment also remained fairly constant at about 30 C. Day temperatures in the hot environment varied between 37 and 39 C.

Photosynthetically active radiation (PAR) averaged about 700 $\mu Em^{-2}sec^{-1}$ during the daily 10-hour light period.

Leaf Expansion

The regression equations in Table 39 were used to estimate leaf area from measurements of leaf lengths and widths. Cumulative leaf area for the three sorghum genotypes is presented in Table 43.

In general cumulative leaf area declined with water stress for all genotypes in all environments. The only exception was genotype RS 626 in environment 3 (hot) where cumulative leaf area under control (non-water stressed) conditions was smaller than under -3 or -4.5 bars of water stress. This was due to die-back of leaves which mostly affected control plants of genotype RS 626 in environment 3. The greatest reductions in leaf area with water stress were in environments 1 (cool) and 2 (transferred from hot to cool). Exposure to elevated temperatures resulted in increases in

Figure 15. Relative humidity (%) and temperature (C) in the two controlled environmental chambers of experiment 6 averaged over a 5-day period.

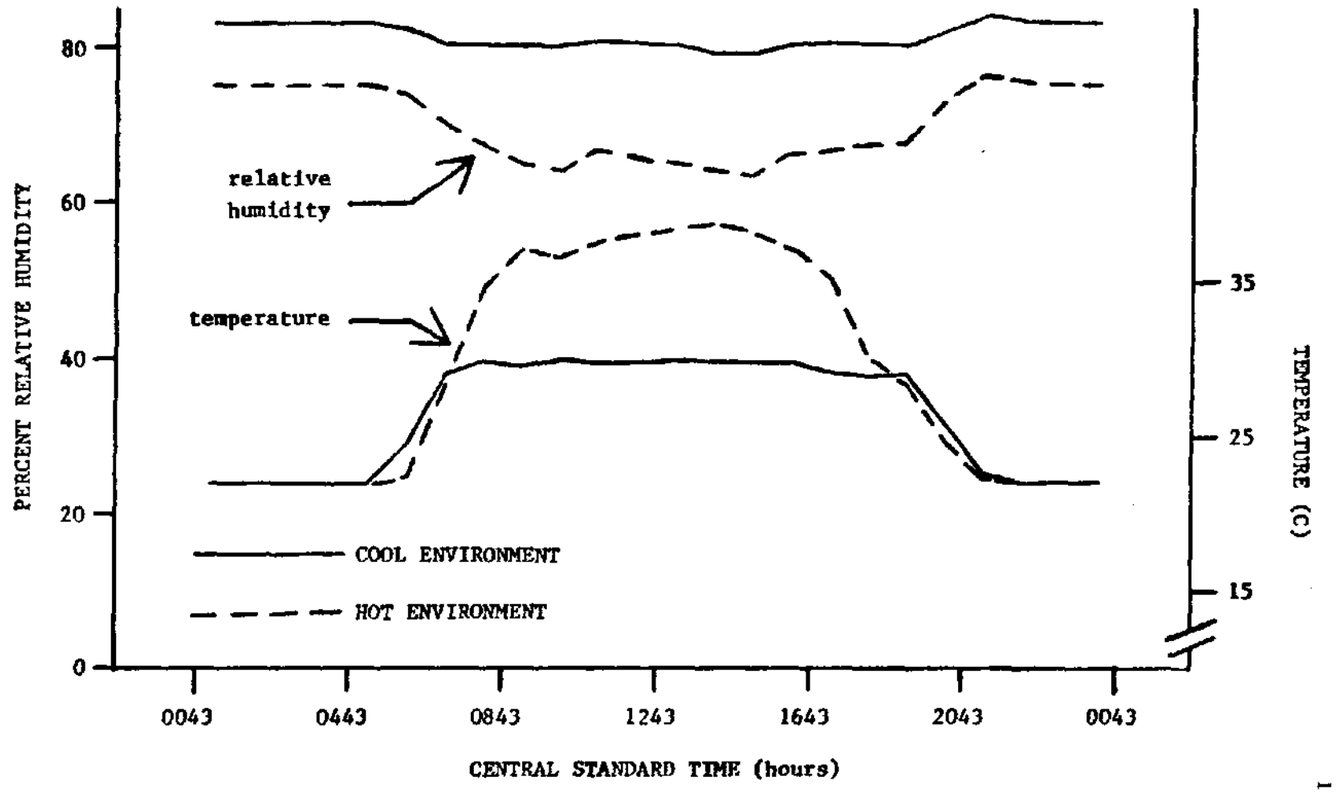


Table 43. Cumulative leaf area (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Leaf Area			
1	0	188 (100)abc[1,2]	209 (111)ab	263 (140)a	220 (117)a[3]
	-3	99 (53)bcd	153 (81)abcd	162 (86)abcd	138 (73)a
	-4.5	87 (46)cd	58 (31)d	151 (80)abcd	99 (53)a
	mean	125 (66)b[4]	140 (74)ab	192 (102)a	
2	0	205 (109)ab	171 (91)ab	252 (134)a	209 (111)a
	-3	177 (94)ab	140 (74)bc	196 (104)ab	171 (91)a
	-4.5	71 (38)c	135 (72)bc	146 (78)bc	117 (62)a
	mean	151 (80)a	149 (79)a	198 (105)a	
3	0	216 (115)ab	259 (138)a	124 (66)cd	200 (106)a
	-3	164 (87)bcd	205 (109)abc	268 (143)a	212 (113)a
	-4.5	135 (72)bcd	101 (54)d	167 (89)bcd	134 (71)a
	mean	172 (91)a	188 (100)a	186 (99)a	
4	0	165 (88)bc	175 (93)b	299 (159)a	213 (113)a
	-3	142 (76)bc	174 (93)b	274 (146)a	197 (105)a
	-4.5	106 (56)c	126 (67)bc	128 (68)bc	120 (64)a
	mean	137 (73)b	158 (84)b	233 (124)a	

Overall Means

Environment	Leaf area	Water stress	Leaf area	Genotype	Leaf area
1	152 (81)a[3]	0	210 (112)a	121	146 (78)b
2	166 (88)a	-3	179 (95)a	160	159 (85)b
3	182 (97)a	-4.5	118 (63)b	RS 626	202 (107)a
4	176 (94)a				

[1] Numbers in parentheses are leaf area expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

leaf area for all genotypes and under all water stress levels (compare environments 1 and 3, Table 43). This response was also observed in Experiment 1 but not in Experiment 5. The day temperature of 40 C in environment 3 in the latter experiment may have been too high for the 2- to 3- week old sorghum seedlings.

Genotypic differences in cumulative leaf area were significant only under control (non-water stressed) and -3 bars of water stress in environment 4 (transferred from cool to hot).

In environments 1 (cool) and 3 (hot) genotype 160 showed the greatest decrease in leaf area at -4.5 bars of water stress but it showed greater stability than either genotype 121 or RS 626 in environments 2 (transferred from hot to cool) and 4 (transferred from cool to hot). Average cumulative leaf area was larger in environments 3 and 4 than in environments 1 and 2 but the differences were not significant. Leaf area duration was greater in environments 1 and 2, however, because the elevated temperatures in the hot environment hastened leaf senescence in plants in environments 3 and 4.

Photosynthesis

Net photosynthetic rates measured 18 and 25 days after emergence (6 and 13 days after relief of water stress) are presented in Tables 44 and 44a, respectively.

In the first set of measurements of photosynthetic rates

Table 44. Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 18 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	Genotype 160	Genotype RS 626	Mean
		Net Photosynthetic Rates			
1	0	45.4 (100)a[1,2]	33.7 (74)a	29.3 (65)a	35.1 (77)a[3]
	-3	38.5 (85)a	36.7 (81)a	19.5 (43)a	31.6 (70)a
	-4.5	41.0 (90)a	-- --	24.8 (55)a	31.3 (69)a
	mean	41.6 (92)a[4]	35.2 (78)a	25.2 (56)a	
2	0	18.0 (40)a	7.7 (17)a	28.6 (63)a	21.0 (46)a
	-3	48.3 (106)a	46.0 (101)a	48.2 (106)a	47.7 (105)a
	-4.5	-- --	33.5 (74)a	34.1 (75)a	33.9 (75)a
	mean	33.1 (73)a	33.3 (73)a	37.3 (82)a	
3	0	19.6 (43)a	41.1 (91)a	43.8 (96)a	35.7 (79)ab
	-3	21.4 (47)a	42.1 (93)a	31.8 (70)a	31.8 (70)b
	-4.5	58.9 (130)a	49.7 (109)a	44.7 (98)a	49.5 (109)a
	mean	28.1 (62)a	42.9 (94)a	40.1 (88)a	
4	0	43.4 (96)a	36.8 (81)a	49.5 (109)a	44.0 (97)a
	-3	58.3 (128)a	28.1 (62)a	40.3 (89)a	41.9 (92)a
	-4.5	-- --	30.0 (66)a	27.4 (60)a	28.7 (63)a
	mean	49.3 (109)a	31.9 (70)a	42.4 (93)a	

Overall Means

Environment	PS rate	Water stress	PS rate	Genotype	PS rate
1	32.9 (72)a[3]	0	34.3 (76)a	121	38.0 (84)a
2	35.0 (77)a	-3	39.1 (86)a	160	36.3 (80)a
3	37.6 (83)a	-4.5	36.7 (81)a	RS 626	35.8 (79)a
4	41.4 (91)a				

[1] Numbers in parentheses are photosynthetic rates expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

(Table 44) differences in response to water stress treatments were significant only when averaged over genotypes in environment 3. The trend was similar to that observed in Experiment 5, with photosynthetic rates under -4.5 bars of water stress being greater than the controls or those subjected to -3 bars of water stress (Table 44).

In the second set of measurements (Table 44a) average photosynthetic rates under -3 bars of water stress were generally higher than under controls (non-water stressed) or under -4.5 bars of water stress but differences were significant only when averaged over all environments.

Average photosynthetic rates were greater in environments 1 and 4 than in environment 3 (Table 44a).

Because of less leaf senescence in the cool environment total photosynthesis was probably greater in environments 1 and 2 than in environments 3 and 4. This is illustrated in Figure 16 where the concentrations of carbon dioxide (CO_2) in the air entering and leaving the two controlled environmental chambers is plotted against time of day. The concentrations of CO_2 in air leaving the cool environment was less than that in air leaving the hot environment during the light period and for some hours after the lights were turned off (Figure 16). This indicates greater total photosynthesis and, at least for a few hours after the lights went off, less total dark respiration in the cool environment than in the hot environment.

Table 44a. Net photosynthetic rates (mg dm^{-2} hr^{-1}) measured 25 days after emergence for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	Genotype 160	Genotype RS 626	Mean
		Net Photosynthetic Rates			
1	0	40.2 (100)a[1,2]	47.8 (119)a	34.9 (87)a	39.0 (97)a[3]
	-3	41.2 (102)a	42.1 (105)a	41.2 (102)a	41.5 (103)a
	-4.5	19.9 (50)a	50.8 (126)a	19.7 (49)a	24.1 (62)a
	mean	35.5 (88)a[4]	45.0 (112)a	31.9 (79)a	
2	0	31.8 (79)a	24.3 (60)a	21.8 (54)a	26.2 (65)a
	-3	30.7 (76)a	42.5 (106)a	35.9 (89)a	37.1 (92)a
	-4.5	11.4 (28)a	38.6 (96)a	40.3 (100)a	32.4 (81)a
	mean	25.7 (64)a	36.5 (91)a	32.7 (81)a	
3	0	21.9 (54)a	20.5 (51)a	41.5 (103)a	28.7 (71)a
	-3	20.5 (51)a	27.2 (68)a	45.1 (112)a	30.9 (77)a
	-4.5	20.4 (51)a	19.6 (49)a	8.6 (21)a	16.2 (40)a
	mean	20.9 (52)a	22.8 (57)a	34.6 (86)a	
4	0	38.6 (96)a	33.3 (83)a	43.7 (109)a	39.2 (98)a
	-3	45.4 (113)a	20.0 (50)a	51.2 (130)a	40.6 (101)a
	-4.5	24.5 (61)a	25.1 (62)a	35.3 (88)a	27.4 (68)a
	mean	34.5 (86)a	26.0 (65)a	44.4 (110)a	

Overall Means

Environment	PS rate	Water stress	PS rate	Genotype	PS rate
1	36.2 (90)a[3]	0	32.9 (82)ab	121	29.3 (73)a
2	31.9 (79)ab	-3	37.4 (93)a	160	31.5 (78)a
3	26.3 (65)b	-4.5	25.9 (64)b	RS 626	35.7 (89)a
4	35.4 (88)a				

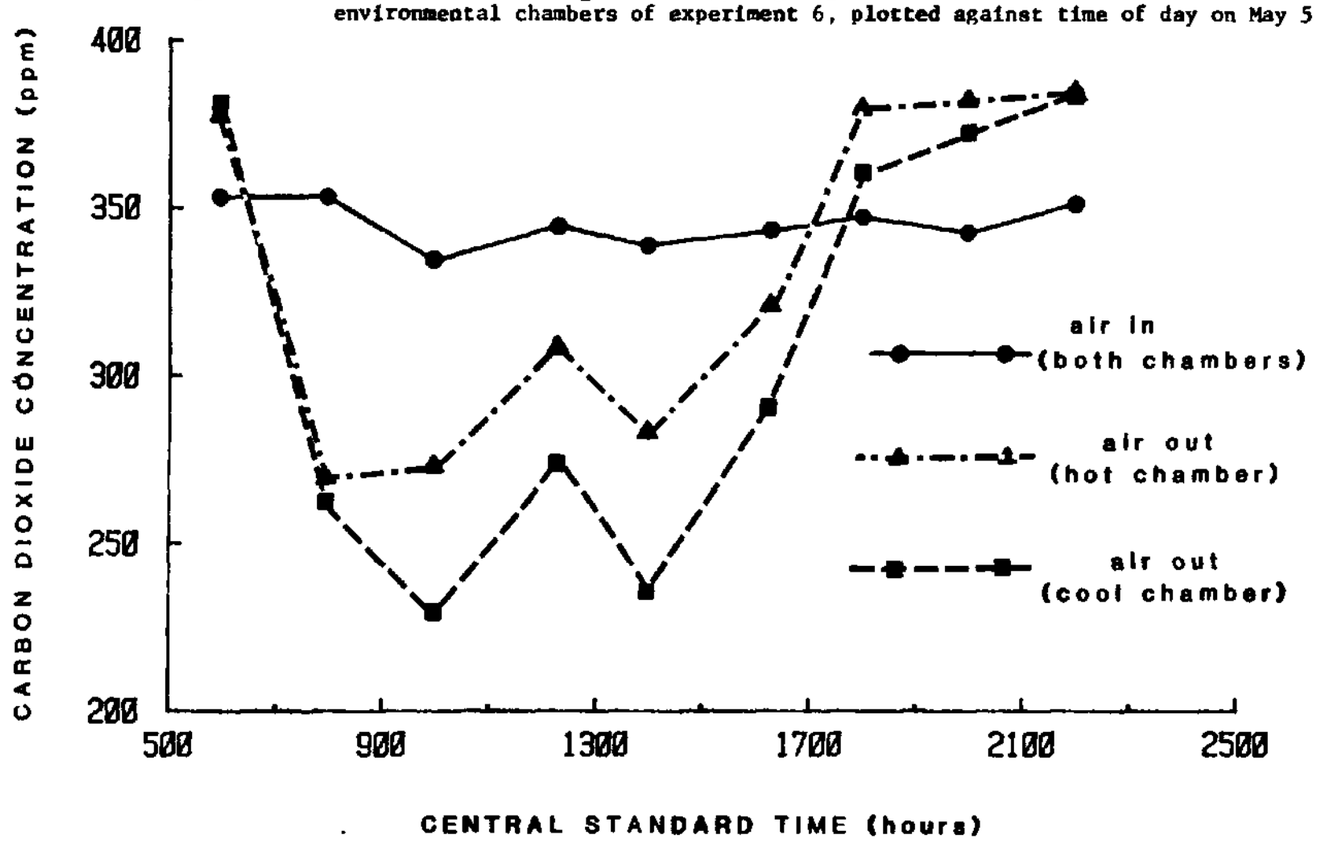
[1] Numbers in parentheses are photosynthetic rates expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Figure 16. Concentration of CO_2 in air (ppm) going into and coming out of the two controlled environmental chambers of experiment 6, plotted against time of day on May 5 1981.



Dry Matter Accumulation

Rates of dry matter accumulation between 19 and 26 days after emergence (between 7 and 14 days after relief of water stress) is presented in Table 45. These rates were calculated from the dry weights in Appendix Tables A6 and A7. Dry matter accumulation rates declined with water stress for all genotypes in all four environments. The only exception was genotype RS 626 in environment 3 where the accumulation rate under -3 bars of water stress was higher than under control (non-water stressed) or -4.5 bars of water stress. This was because of the die-back of leaves of control plants of RS 626 in environment 3.

Environmental differences in dry matter accumulation rates were not significant but average rates were greatest in environment 4 and lowest in environment 1 (Table 45).

Table 45. Dry matter accumulation rates (mg per day) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		---------Dry Matter Accumulation Rates----------			
1	0	382 (100)a[1,2]	212 (55)ab	314 (82)a	303 (79)a[3]
	-3	106 (28)b	201 (53)ab	207 (54)ab	171 (45)a
	-4.5	106 (28)b	38 (10)b	199 (52)ab	115 (30)a
	mean	198 (52)a[4]	150 (39)a	240 (63)a	
2	0	393 (103)a	206 (54)bc	390 (102)a	330 (86)a
	-3	229 (60)bc	185 (48)c	364 (95)ab	259 (68)a
	-4.5	82 (21)c	146 (38)c	245 (64)abc	158 (41)a
	mean	235 (62)b	179 (47)b	333 (87)a	
3	0	367 (96)a	295 (77)ab	217 (57)bcd	293 (77)a
	-3	177 (46)cde	235 (62)bc	353 (92)a	255 (67)a
	-4.5	145 (38)de	123 (32)e	212 (55)bcd	160 (42)a
	mean	230 (60)a	218 (57)a	261 (68)a	
4	0	299 (78)bc	293 (77)bc	457 (120)a	350 (92)a
	-3	246 (64)bcd	216 (57)cd	372 (97)ab	278 (73)a
	-4.5	122 (32)d	206 (54)cd	157 (41)d	162 (42)a
	mean	222 (58)b	238 (62)b	329 (86)a	

Overall Means

Environment	Accum. rates	Water stress	Accum. rates	Genotype	Accum. rates
1	196 (51)a[3]	0	319 (84)a	121	221 (58)b
2	249 (65)a	-3	241 (63)a	160	196 (51)b
3	236 (62)a	-4.5	149 (39)b	RS 626	291 (76)a
4	263 (69)a				

[1] Numbers in parentheses are dry matter accumulation rates expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

EXPERIMENT 7

Day and night temperatures (C) and relative humidity (%) for the four environments is presented in Table 46. It will be noticed that environments 2, 3, and 4 in this experiment are markedly different from those in experiments 5 and 6, in that the elevated temperatures are lower and the duration of exposure shorter in this study. Temperatures were elevated in environment 2 only during the four-day water stress period; in environment 3 during the 4-day water stress period and a 4-day post-water stress period; and in environment 4 only during the 4-day post-water stress period. At all other times day and night temperatures in all environments were maintained near 30 and 20 C, respectively (Table 46). Percent relative humidity was higher in environments 3 and 4 than in environments 1 and 2 from 23 days after emergence to the end of the study (Table 46). This was due to failure of the humidity control mechanism in one of the two controlled environmental chambers.

Radiant energy during the daily 12-hour light period from 0600 to 1800 hrs CST averaged about 700 $\mu EM^{-2}sec^{-1}$.

Leaf Development

No differences were observed in the rate of leaf appearance between environments or between water stress treatments. There were some genotypic differences in the rate of new leaf appearance in all environments. Leaves of genotype 160

Table 46. Day and night temperatures (C) and relative humidity (%) in the four environments of experiment 7 averaged over varying number of days after emergence.

Days after emergence	ENVIRONMENTS							
	1		2		3		4	
	Day[1]	Night[1]	Day	Night	Day	Night	Day	Night
	Temperature (C)							
0-5	29.6	20.3	29.6	20.3	29.6	20.3	29.6	20.3
6-10	29.1	21.0	29.1	21.0	29.1	21.0	29.1	21.0
11-17	29.4	20.7	29.4	20.7	29.4	20.7	29.4	20.7
18-22[2]	29.4	20.1	34.4	20.0	34.4	20.0	29.4	20.1
23-26	29.2	20.5	29.2	20.5	33.0	19.9	33.0	19.9
27-32	29.4	20.3	29.4	20.3	29.3	20.1	29.3	20.1
33-38	29.3	20.0	29.3	20.0	29.3	19.7	29.3	19.7
39-44	29.1	19.9	29.1	19.9	29.0	19.3	29.0	19.3
45-50	30.0	20.2	30.0	20.2	29.5	20.0	29.5	20.0
	Relative humidity (%)							
0-5	50.8	61.3	50.8	61.3	50.8	61.3	50.8	61.3
6-10	54.3	82.7	54.3	82.7	54.3	82.7	54.3	82.7
11-17	51.7	64.4	51.7	64.4	51.7	64.4	51.7	64.4
18-22[2]	50.1	55.4	64.1	72.4	64.1	72.4	50.1	55.4
23-26	54.2	54.9	54.2	54.9	73.0	77.3	73.0	77.3
27-32	57.9	60.1	57.9	60.1	76.7	79.0	76.7	79.0
33-38	59.6	62.4	59.6	62.4	78.4	79.4	78.4	79.4
39-44	59.9	62.2	59.9	62.2	78.2	80.4	78.2	80.4
45-50	46.2	53.5	46.2	53.5	59.4	70.7	59.4	70.7

[1] Day temperature and relative humidity were 14-hour averages from 0600 to 2000 hours Central Standard Time (CST); and night temperature and relative humidity were 10-hour averages from 2000 to 0600 hours CST.

[2] Water stress was applied during this 4-day period.

appeared about 2 days earlier than comparable leaves of genotype RS 626 which in turn appeared an average of about 2.5 days earlier than those of genotype 121.

Leaf area was estimated as in Experiments 5 and 6 using the regression equations in Table 39.

Area of leaves expanded before the imposition of water stress and that of leaves expanded during the stress period are presented in Tables 47a and 47b, respectively. In both tables genotype 160 had significantly larger leaf area than genotypes RS 626 and 121. This was largely due to more rapid rate of leaf appearance.

Environmental differences in leaf area were not significant before or during the water stress period.

Before water stress was imposed, leaf area of plants that were scheduled to be water stressed were larger than the controls in both environments 1 and 3 but the difference was significant only in environment 3. In environments 2 and 4 plants that were scheduled to be water stressed at -3 bars had larger leaf area than those scheduled to be water stressed at -4.5 bars but the difference was significant only in environment 2 (Table 47a).

Area of leaves expanded during the period of water stress was significantly greater for the controls than for water stressed plants in environments 1 and 3 (Table 47b). Thus water stress must have slowed the leaf expansion rate to reverse the trends in leaf area observed before imposition

Table 47a. Area of leaves fully expanded (cm^2) before various levels of water stress were imposed on three sorghum genotypes grown under four temperature environments.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Leaf Area			
1	0	129 (100)d[1,2]	170 (132)bc	137 (106)d	145 (112)b[3]
	-3	142 (110)d	186 (144)ab	146 (113)cd	158 (122)a
	-4.5	130 (101)d	204 (158)a	145 (112)cd	160 (124)a
	mean	134 (104)b[4]	187 (145)a	143 (111)b	
2	-3	160 (124)b	199 (154)a	145 (112)b	168 (130)a
	-4.5	141 (109)b	190 (147)a	147 (114)b	159 (123)b
	mean	150 (116)b	195 (151)a	146 (113)b	
3	0	135 (105)b	174 (135)a	138 (107)b	149 (116)a
	-3	142 (110)b	177 (137)a	143 (111)b	154 (119)a
	-4.5	138 (107)b	172 (133)a	140 (109)b	150 (116)a
	mean	138 (107)b	174 (135)a	140 (109)b	
4	-3	141 (109)bc	191 (148)a	155 (120)b	162 (126)a
	-4.5	127 (98)c	179 (139)a	140 (109)c	148 (115)a
	mean	134 (104)c	185 (143)a	148 (115)b	

Overall Means

Environment	Leaf area	Water stress	Leaf area	Genotype	Leaf area
1	154 (119)a[3]	0	147 (114)c	121	138 (107)b
2	164 (127)a	-3	161 (125)a	160	184 (143)a
3	151 (117)a	-4.5	154 (119)b	RS 626	144 (112)b
4	155 (120)a				

[1] Numbers in parentheses are leaf area expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 47b. Area of leaves fully expanded (cm^2) during the water stress period for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Leaf Area			
1	0	314 (100)bc[1,2]	336 (107)ab	313 (100)bc	321 (102)a[3]
	-3	262 (83)d	364 (116)a	269 (86)cd	298 (95)b
	-4.5	298 (95)bcd	370 (118)a	282 (90)cd	316 (101)ab
	mean	292 (93)b[4]	356 (113)a	288 (92)b	
2	-3	339 (108)a	356 (113)a	289 (92)c	328 (104)a
	-4.5	322 (103)ab	336 (107)a	297 (95)bc	318 (101)a
	mean	331 (105)a	346 (110)a	293 (93)b	
3	0	333 (106)ab	351 (112)a	315 (100)bc	333 (106)a
	-3	312 (99)bc	332 (106)ab	294 (94)cd	313 (100)b
	-4.5	252 (80)e	297 (95)cd	277 (88)de	275 (88)c
	mean	299 (95)b	326 (104)a	295 (94)b	
4	-3	290 (92)b	321 (102)a	266 (85)bc	292 (93)a
	-4.5	268 (85)bc	322 (103)a	252 (80)c	281 (89)a
	mean	279 (89)b	321 (102)a	259 (82)c	

Overall Means

Environment	Leaf area	Water stress	Leaf area	Genotype	Leaf area
1	312 (99)a[3]	0	327 (104)a	121	299 (95)b
2	323 (103)a	-3	308 (98)b	160	338 (108)a
3	307 (98)a	-4.5	298 (95)c	RS 626	285 (91)c
4	287 (91)a				

[1] Numbers in parentheses are leaf area expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Differences in cumulative leaf area between water stress

Table 47c. Ratio of leaf area expanded during the water stress period to leaf area expanded up to the end of the water stress period for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Ratio			
1	0	.71 (100)a[1,2]	.66 (93)b	.70 (99)a	.69 (97)a[3]
	-3	.65 (92)b	.66 (93)b	.65 (92)b	.65 (92)b
	-4.5	.70 (99)a	.64 (92)b	.66 (93)b	.67 (94)b
	mean	.68 (96)a[4]	.66 (93)b	.67 (94)b	
2	-3	.68 (96)a	.64 (92)b	.67 (94)ab	.66 (93)a
	-4.5	.70 (99)a	.64 (92)b	.67 (94)ab	.67 (94)a
	mean	.69 (97)a	.64 (92)b	.67 (94)a	
3	0	.71 (100)a	.67 (94)bc	.70 (99)ab	.69 (97)a
	-3	.69 (97)ab	.65 (92)cd	.67 (94)bc	.67 (94)b
	-4.5	.65 (92)cd	.63 (89)d	.66 (92)bcd	.65 (92)c
	mean	.68 (96)a	.65 (92)b	.68 (96)a	
4	-3	.67 (94)a	.63 (89)b	.63 (89)b	.64 (92)a
	-4.5	.68 (96)a	.64 (92)b	.64 (92)b	.65 (92)a
	mean	.68 (96)a	.63 (89)b	.64 (92)b	

Overall Means

Environment	Ratio	Water stress	Ratio	Genotype	Ratio
1	.67 (94)a[3]	0	.69 (97)a	121	.68 (96)a
2	.67 (94)a	-3	.66 (93)b	160	.66 (93)b
3	.67 (94)a	-4.5	.66 (93)b	RS 626	.65 (92)c
4	.65 (92)a				

1 Numbers in parentheses are ratios expressed as percentages of genotype 121, water stress 0, environment 1.

2 Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

3 Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

4 Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Table 47d. Total cumulative leaf area (cm^2) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Leaf Area			
1	0	872 (100)b[1,2]	1090 (125)ab	1101 (126)ab	1021 (117)a[3]
	-3	895 (103)b	1151 (132)a	1002 (115)ab	1016 (117)a
	-4.5	900 (103)b	1158 (133)a	1045 (120)ab	1034 (119)a
	mean	889 (103)b[4]	1133 (130)a	1049 (120)a	
2	-3	908 (104)c	1198 (137)a	1191 (137)a	1099 (126)a
	-4.5	951 (109)bc	1079 (124)ab	1020 (117)bc	1016 (117)b
	mean	929 (107)b	1138 (131)a	1106 (127)a	
3	0	764 (88)d	933 (107)abc	960 (110)abc	886 (102)a
	-3	878 (101)bcd	997 (114)ab	1002 (115)ab	959 (110)a
	-4.5	834 (96)cd	1049 (120)a	1042 (119)a	975 (112)a
	mean	825 (95)b	993 (114)a	1002 (115)a	
4	-3	726 (83)b	913 (105)a	932 (107)a	857 (98)a
	-4.5	749 (86)b	964 (111)a	871 (100)a	862 (99)a
	mean	738 (85)b	939 (108)a	902 (103)a	

Overall Means

Environment	Leaf area	Water stress	Leaf area	Genotype	Leaf area
1	1024 (117)a[3]	0	953 (109)a	121	848 (97)b
2	1058 (121)a	-3	983 (113)a	160	1053 (121)a
3	940 (108)b	-4.5	972 (111)a	RS 626	1017 (117)a
4	859 (99)b				

[1] Numbers in parentheses are leaf area expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

treatments were significant only in environment 2 where plants subjected to -3 bars of water stress had significantly larger total leaf area than those subjected to -4.5 bars of water stress. Total cumulative leaf area was significantly larger in environments 1 and 2 than in environments 3 and 4 (Table 47d). This was likely due to temperature stress caused by differences in percent relative humidity between the two controlled environmental chambers from 23 days after emergence. Due to a failure in the control mechanism the % relative humidity in the 'hot' chamber was quite high (more than 70%) both day and night during this period (Table 46). This would be expected to slow down transpiration and cause elevated plant temperatures which may in turn have interferred with plant metabolism and growth.

Plant Dry Matter

Plant dry matter at harvest is presented in Table 48. There were no significant water stress treatment differences in any of the environments. In environments 2, 3, and 4, genotype RS 626 accumulated significantly more dry matter than genotypes 121 and 160. Mean plant dry matter for all genotypes was significantly higher in environments 1 and 2 than in environments 3 and 4 (Table 48). This may again reflect the differences in % relative humidity between the two controlled environmental chambers rather than differences due to the temperature treatments.

Table 48. Total dry matter (g per plant) for three sorghum genotypes grown under four temperature environments and subjected to various levels of water stress.

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Total Dry Matter			
1	0	7.9 (100)a[1,2]	7.4 (94)a	9.3 (118)a	8.2 (104)a[3]
	-3	8.1 (103)a	7.9 (100)a	8.4 (106)a	8.1 (103)a
	-4.5	7.9 (100)a	8.0 (101)a	8.4 (106)a	8.1 (103)a
	mean	7.9 (100)a[4]	7.8 (99)a	8.7 (110)a	
2	-3	8.0 (101)cd	8.4 (106)bcd	10.3 (130)a	8.9 (113)a
	-4.5	9.5 (120)ab	7.6 (96)d	9.0 (114)bc	8.7 (110)a
	mean	8.7 (110)b	8.0 (101)b	9.6 (122)a	
3	0	6.2 (78)c	6.5 (82)bc	7.4 (94)abc	6.7 (85)a
	-3	7.8 (99)ab	6.8 (86)bc	7.9 (100)ab	7.5 (95)a
	-4.5	7.1 (90)abc	7.2 (91)abc	8.4 (106)a	7.6 (96)a
	mean	7.0 (89)b	6.8 (86)b	7.9 (100)a	
4	-3	6.4 (81)ab	6.3 (80)b	7.4 (94)a	6.7 (85)a
	-4.5	6.4 (81)ab	6.7 (85)ab	7.2 (91)ab	6.8 (86)a
	mean	6.4 (81)b	6.5 (82)b	7.3 (92)a	

Overall Means

Environment	Total dry matter	Water stress	Total dry matter	Genotype	Total dry matter
1	8.1 (103)a[3]	0	7.5 (95)a	121	7.5 (95)b
2	8.8 (111)a	-3	7.8 (99)a	160	7.3 (92)b
3	7.3 (92)b	-4.5	7.8 (99)a	RS 626	8.4 (106)a
4	6.7 (85)b				

[1] Numbers in parentheses are total dry matter expressed as percentages of genotype 121, water stress 0, environment 1.

[2] Means in the same row or column followed by the same letter(s) are not significantly different at p = .05 by Duncan's New Multiple Range Test (DNMR).

[3] Means in the same column followed by the same letter(s) are not significantly different at p = .05 by DNMR.

[4] Means in the same row followed by the same letter(s) are not significantly different at p = .05 by DNMR.

Interactions of Water Stress and Temperature

Interactions of water stress and environment were significant only for area of leaves expanded during the water stress period. This was because under control (non-water stressed) conditions and under -3 bars of water stress, exposure to elevated temperatures caused an increase in leaf area while under -4.5 bars of water stress it caused a decrease in leaf area compared to the low temperature environment (Table 47b). A similar behavior in leaf area was also observed in Experiments 1 and 6.

SUMMARY

Both water stress and elevated day temperatures (more than 35 C) reduced the rate of leaf appearance in sorghum especially when such elevated day temperatures were accompanied by night temperatures of less than 20 C. Exposure to about 35 C day temperatures and 22 to 23 C night temperatures hastened the rate of leaf appearance possibly because of compensatory leaf growth at night. Four days without irrigation had no effect on leaf appearance rate but 8 and 12 days without irrigation reduced both the rate of leaf appearance and the final leaf size of 7-week old plants. Water stress of as mild as -3 bars (-0.3 MPa) was found to reduce the final leaf size of 9-day old sorghum seedlings growing in a cool or hot environment. While elevated day temperatures accompanied by less than 20 C night temperatures reduced leaf appearance rate of 7-week old plants the final leaf size was increased over those of plants grown in a cool environment under non water stressed conditions. The same was true of 9-day old seedlings under non water stressed conditions and under -3 bars (-0.3 MPa) of water stress. Under -4.5 bars (-0.45 MPa) of water stress the reduction in final leaf size of 9- to 18-day old seedlings was greater in a hot environment than in a cool environment. Total cumulative leaf area of sorghum seedlings was significantly reduced by elevated temperatures accompanying or following -3 and -4.5

bars of water stress but not by elevated temperatures preceeding these levels of water stress. Significant genotypic differences were observed in the response of leaf extension and expansion to elevated temperatures. When plants were exposed to day temperatures of 35 C, area of a representative leaf was increased by 5% for the sorghum hybrid Wheatland X SC118, but it was reduced by 27% and 11% for the hybrids Martin X SC33-9-2-2-2 and RS 626, respectively, compared to those of plants grown in a 30 C environment. Under non-water stressed conditions cumulative leaf area of sorghum lines 121 and 160 were increased by 15 and 24%, respectively, by exposure to temperatures of 38 C over those of plants grown under 30 C. Leaf area of sorghum hybrid RS 626 was reduced by 53% but this was mostly due to die back of leaves which could have been partially due to the elevated temperatures. Under conditions of -3 and -4.5 bars of water stress leaf area of all three genotypes was increased by exposure to the high temperatures. These increases averaged 61%, 45%, and 39%, for the genotypes 121, 160, and RS 626, respectively. In another experiment (Experiment 7) where elevated temperatures of 37 C were coupled with high (70-80%) relative humidity cumulative leaf area of all three genotypes were reduced compared to those of plants grown in a 30 C environment and 50-60% relative humidity. These decreases were 7, 12, and 6% for 121, 160, and RS 626, respectively.

Trends in photosynthetic rates were not consistent

enough to draw any conclusions from. Water stress of -3 and -4.5 bars in general increased the leaf photosynthetic rates of sorghum seedlings during the post stress period. Total canopy photosynthesis was, however, likely greater under non water stressed conditions because of the greater leaf area and less senescence of lower leaves. This was evidenced by the greater dry matter accumulation rates under non water stressed conditions than under -3 and -4.5 bars of water stress. Exposure to temperatures of 40 C caused a decrease in the net photosynthetic rates of sorghum seedlings whether or not such temperatures were accompanied by water stress, but temperatures of only 2 C lower (38 C) caused an increase in the net photosynthetic rates over those of plants grown in a 30 C environment, especially under -3 and -4.5 bars of water stress.

Under non water stressed conditions exposure to elevated temperatures hastened bloom by up to 4 days but bloom was delayed by elevated temperatures when plants were subjected to even 4 days of water stress. Four days without irrigation hastened bloom in plants grown in a cool environment but 8 and 12 days without irrigation delayed bloom in plants grown in either a cool or a hot environment. Physiological maturity was also hastened by exposure to elevated temperatures during the grain filling stage in well watered plants and in plants water stressed for 4 days. Four days without irrigation had no effect on the number of days taken to

reach physiological maturity (black layer formation) as compared to the controls. When coupled with elevated temperatures (35 C) water stress of -6 bars (-0.6 MPa) hastened physiological maturity by up to 3 days. Eight and 12 days without irrigation delayed physiological maturity by 3 to 12 days probably due to cessation of growth during the stress period. These results were taken to indicate that under the conditions of these experiments temperature rather than water stress caused premature cessation of grain growth in sorghum. Further experimentation may be required to verify this finding.

Only 8 and 12 days without irrigation caused tillering in plants grown in a cool environment but even 4 days without irrigation caused tillering in a hot environment. This was thought to be a reaction to the retardation in growth of the main shoot rather than a direct effect of temperature or water stress.

Under non water stressed conditions and under 4 days of water stress, exposure to elevated temperatures (35 C) during panicle initiation and development led to larger panicles and greater seed numbers, thus increasing grain yields. This treatment increased panicle weight, seed numbers and grain yield by 30, 16, and 34%, respectively, under non-water stressed conditions, and by 36, 15, and 40% respectively under 4 days of water stress, compared to plants grown in a cool (30 C) environment throughout. Under

8 days of water stress panicle weight was reduced by 3%, number of seeds by 11% and grain yield by 5%. Exposure to elevated temperatures caused declines of 42, 56, and 49% in panicle weight, seed numbers and grain yield, respectively, when the number of days between irrigations increased to 12 days. Exposure to elevated temperatures during panicle development thus proved beneficial under non-water stressed conditions and under conditions of limited water deficits, but it was highly detrimental under an extended period of water stress. Panicle weights, seed numbers and yield generally decreased in all environments with increase in the number of days between irrigations from 4 to 12 days. Averaged over the four hybrids, panicle weights decreased by 10, 33, and 66% in the cool environment and by 12, 57, and 92% in the hot environment with 4, 8, and 12 days of water stress, respectively. Seed numbers decreased by 9, 36, and 68% in the cool environment and by 21, 68, and 97% in the hot environment with 4, 8, and 12 days of water stress, respectively. Grain yield decreased by 11, 36, and 74% in the cool environment and by 16,69, and 96% in the hot environment, with 4, 8, and 12 days of water stress, respectively. Water stress of -4 bars (-0.4 MPa), osmotically controlled with polyethylene glycol, caused a significant (17%) increase in panicle weight of plants grown in a cool (30 C) environment but the increase (5%) was not significant for plants grown in a hot (35 C) environment. Exposure to elevated temperature

during the boot stage reduced panicle weight and seed numbers possibly due to floret abortion. Seed size increased with exposure to elevated temperatures during the late vegetative and early reproductive stages. Seed size was also increased by increasing number of days between irrigations but these increases were not enough to offset the large decreases in seed numbers. Seed numbers of plants grown in a cool or a hot environment were not affected by water stress of -4 or -6 bars. Water stress of -4 bars had no significant effect on the seed size of plants grown in either environment but -6 bars of water stress caused slight but significant decreases in seed size of plants grown in both environments. This caused grain yields to be higher under -4 bars of water stress than under well watered conditions or under -6 bars of water stress in both environments.

Heat tolerance tests showed discs from older leaves to be significantly more tolerant than discs from younger (newly expanded) leaves. Both water stress and exposure to elevated temperatures increased heat and desiccation tolerance of leaves as determined by the electrical conductivity method. Although 4 days of water stress did not affect the growth and yield of plants, the conductivity tests showed them to be more tolerant of heat and desiccation than the controls indicating a certain degree of increased membrane stability due to "hardening". There were significant genotypic differences in the degree of heat and desiccation tolerance

but these differences disappeared with plant age, with increased water stress, and with extended exposure to elevated temperatures. Heating at 53.5 C caused 18% less injury to leaf tissue of plants that had been water stressed for 4 days compared to leaf tissue of non water stressed plants. Similarly, desiccation at -16 bars (-1.6 MPa), on the average, caused 11% less injury to leaf tissue of plants that had been water stressed for 4 days compared to leaf tissue of control plants.

Significant interactions between water stress and temperature were observed with water stress of 4 to 12 days without irrigation in 8-liter pots filled with a 1:1:1 mixture of soil, sand, and peat moss, but not when water stress levels were -3 to -6 bars (osmotically controlled with polyethylene glycol). Under non-water stressed conditions and under 4 days without irrigation or -4 bars of osmotically controlled water stress, exposure to elevated temperatures accelerated plant growth and development and increased yield of grain and total dry matter by up to 40 and 32%, respectively. When water stress was moderate or severe, elevated temperatures delayed plant development and drastically reduced grain yields by up to 80%. Because such severe water stress greatly induced tillering in the hot environment the decrease in total dry matter (20%) was less under severe stress, than under non-water stressed conditions.

Although extensive research has been done on the effects

of water and high temperature stress on various aspects of plant growth and development, literature on the interactions of the two stresses is very limited. Under the conditions of these series of experiments some complex interactions between water stress and high temperatures were observed. Although these studies were conducted under controlled conditions similar interactions would be expected to occur in the field especially in regions where elevated temperatures (35 C and above) are quite common sometime during the growing season. Further experimentation is required to look at these interactions more closely both in the field and under controlled conditions.

LITERATURE CITED

Acevedo, E., T. C. Hsiao, and D. W. Hendersen. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

Alexandrov, V. Y. 1964. Cytophysiological and cytoecological investigations of heat resistance of plant cells toward the action of high and low temperature. Quarterly Rev. Biol. 39:35-77.

Asana, R. D. and F. R. Williams. 1965. The effect of temperature on grain development in wheat. Aust. J. Agric. Res. 16:1-13.

Bennett, J. M. 1979. Responses of grain sorghum (Sorghum bicolor L. Moench) to osmotic stresses imposed at various growth stages. Ph. D. Thesis, University of Nebraska, Lincoln. 202 p.

Bishnoi, U. R. 1966. A note on the estimation of leaf area in two varieties of sorghum. Annals of Arid Zones 5:255-256.

Bjorkman, O., M. R. Badger, and P. A. Armond. 1980, Response and adaptation of photosynthesis to high temperatures. In N. C. Turner and P. J. Kramer (Eds.). Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, N. Y. pp 233-249.

Blum, A. 1973. Components analysis of yield responses to drought of sorghum hybrids. Expt. Agric. 9:159-167.

Blum, A. 1974a. Genotypic responses in sorghum to drought stress I. Response to soil moisture stress. Crop Sci. 14:361-364.

Blum, A. 1974b. Genotypic responses in sorghum to drought stress II. Leaf tissue water relations. Crop Sci. 14:691-692.

Blum, A. and A. Ebercon. 1976. Genotypic responses in sorghum to drought stress III. Free proline accumulation and drought stress. Crop Sci. 16:428-431.

Blum, A. and C. Y. Sullivan. 1972. A laboratory method for monitoring net photosynthesis in leaf segments under controlled water stress experiments with sorghum. Photosynthetica 6:18-23.

Boyer, J. S. 1970a. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.

Boyer, J. S. 1970b. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46: 236-239.

Boyer, J. S. 1976. Photosynthesis at low water potentials. Phil. Trans. R. Soc. Lond. B. 273:501-512.

Boyer, J. S. and B. L. Bowen. 1970. Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials. Plant Physiol. 45:612-615.

Boyer, J. S. and H. G. McPherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23.

Boyer, J. S. and J. R. Potter. 1973. Chloroplast response to low leaf water potentials I. Role of turgor. Plant Physiol. 51: 989-992.

Brix, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant. 15:10-20.

Brown, K. W. and J. C. Thomas. 1980. The influence of water stress preconditioning on dark respiration. Physiol. Plant. 49:205-209.

Carbon, B. A. 1973. Diurnal water stress in plants grown on a coarse soil. Aust. J. Agric. Res. 24:33-42.

Chrelashvili, M. N. 1941. The influence of water content and carbohydrate accumulation on the energy of photosynthesis and respiration. Biol. Abst. 15:22669.

Claassen, M. M. and R. H. Shaw. 1970. Water deficit effects on corn II. Grain components. Agron. J. 62:652-655.

Clegg, M. D,, C. Y. Sullivan, and J. D. Eastin. 1978. A sensitive technique for the rapid measurement of carbondioxide concentrations. Plant Physiol. 62:924-926.

Contable, G. A. and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits I. Growth, development and yield. Aust. J. Plant Physiol. 5:159-167.

Damptey, H. B. and D. Aspinall. 1976. Water deficit and inflorescence development in Zea mays L. Ann. Bot. 40:23-25.

Davidson, J. L. 1965. Some effects of leaf area control on the yield of wheat. Aust. J. Agric. Res. 16:721-731.

Doley, D. and N. B. A. Trivett. 1974. Effects of low water potential on transpiration and photosynthesis in Mitchell grass (Astrebia lappacea). Aust. J. Plant Physiol. 1:539-550.

Downes, R. W. 1968. The effect of temperature on tillering of grain sorghum seedlings. Aust. J. Agric. Res. 19:59-64.

Downes, R. W. 1970. Effect of light intensity and leaf temperature on photosynthesis and transpiration in wheat and sorghum. Aust. J. Biol. Sci. 23:775-782.

Downes, R. W. 1971. Relationship between evolutionary adaptation and gas exchange characteristics of diverse sorghum taxa. Aust. J. Biol. Sci. 24:843-852.

Downes, R. W. 1972. Effects of temperature on the phenology and grain yield of Sorghum bicolor. Aust. J. Agric. Res. 23:585-594.

Downey, L. A. 1971. Effect of gypsum and drought stress on maize (Zea mays L.) I. Growth, light absorption and yield. Agron J. 63:569-572.

Eastin, J. D. 1972. Photosynthesis and translocation in relation to plant development. In N. G. P. Rao and L. R. House (Eds.) Sorghum in Seventies. Oxford and IBH Pub. Co., New Delhi. pp 214-246.

Eastin, J. D. 1976. Temperature influence on sorghum yield. Proc. 31st Ann. Corn and Sorghum Res. Conf. pp 19-23.

Eck, H. V. and J. T. Musick. 1979a. Plant water stress effects on irrigated grain sorghum 1. Effects on yield. Crop Sci. 19:589-591.

Eck, H. V. and J. T. Musick. 1979b. Plant water stress effects on irrigated grain sorghum 2. Effects on nutrients in plant tissues. Crop Sci. 19:592-598.

El-Sharkawy, M. A. and J. D. Hesketh. 1964. Effects of temperature and water deficit on leaf photosynthetic rates of different species. Crop Sci. 4:514-518.

Fereres, E., E. Acevedo, D. W. Henderson, and T. C. Hsiao. 1978. Seasonal changes in water potential and turgor maintenance in sorghum and maize under water stress. Physiol. Plant. 44:261-267.

Fischer, K. S. and G. L. Wilson. 1971. Studies of grain production in Sorghum vulgare I. The contribution of preflowering photosynthesis to grain yield. Aust. J. Agric. Res. 22:33-37.

Fischer, R. A. 1973. The effect of water stress at various stages of development on yield processes in wheat. In R. O. Slatyer (Ed.). Plant Response to Climatic Factors. UNESCO, Paris. pp 233-241.

Fischer, R. A. and R. M. Hagan. 1965. Plant water relations, irrigation management and crop yield. Expt. Agric. 1:161-177.

Fischer, R. A. and G. D. Kohn. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in wheat crop under conditions of limited soil moisture. Aust. J. Agric. Res. 17:281-295.

Frank, A. B., J. F. Power, and W. O. Willis. 1973. Effects of temperature and plant water stress on photosynthesis, diffusion resistance, and leaf water potential in spring wheat. Agron. J. 65:777-780.

Gallagher, J. N., P. V. Biscoe, and B. Hunter. 1976. Effects of drought on grain growth. Nature, Lond. 264:541-542.

Garrity, D., C. Y. Sullivan, and W. M. Ross. 1982. Alternative approaches to improving grain sorghum productivity under grought stress. In Principles and Methods for Crop Improvement for Drought Resistance: With Emphasis on Rice. Int. Symp., International Rice Research Institute, May 1981. (In press).

Giles, K. L., D. Cohen, and M. F. Beardsell. 1976. Effects of water stress on the ultrastructure of leaf cells of Sorghum bicolor. Plant Physiol. 57:11-14.

Heichel, G. H. and R. B. Musgrave. 1970. Photosynthetic response to drought in maize. Phillip. Agric. 54:102-114.

Henckel, P. A. 1964. Physiology of plants under drought. Ann. Rev. Plant Physiol. 15:363-386.

Henzell, R. G., K. J. McCree, C. H. M. van Bavel, and K. F. Schertz. 1975. Method for screening sorghum genotypes for stomatal sensitivity to water deficits. Crop Sci. 15:516-518.

Hesketh, J. D. 1968. Effect of light and temperature during plant growth on subsequent leaf CO_2 assimilation rates under standard conditions. Aust. J. Biol. Sci. 21:235-241.

Hsiao, T. C., E. Acevedo, and D. W. Henderson. 1970. Maize leaf elongation: Continuous measurements and close dependence on plant water status. Science 168:590-591.

Huffaker, R. C., T. Radin, G. E. Kleinkopf, and E. L. Cox. 1970. Effects of mild water stress on enzymes of nitrate assimilation and of the carboxylative phase of photosynthesis in barley. Crop Sci. 10:471-474.

Hughes, W. F., A. C. Magee, D. Jones, and E. L. Thaxton. 1959. Economics of water management for cotton and grain sorghum production. High Plains. Bull. Texas Agric. Expt. Stat. 931.

Inuyama, S. 1978a. Varietal differences in leaf water potential, leaf diffusive resistance and yield of grain sorghum affected by drought stress. Jpn. J. Crop Sci. 47:255-261.

Inuyama, S. 1978b. Effects of plant densities under two irrigation regimes on leaf water potential, leaf diffusive resistance, and grain yield of grain sorghum. Jpn. J. Crop Sci. 47:596-601.

Inuyama, S. 1980. Effects of the amount of irrigation water on growth and grain yield of grain sorghum. Jpn. J. Crop Sci. 49:226-231.

Jenner, L. F. and A. J. Rathjen. 1975. Factors regulating accumulation of starch in ripening wheat grain. Aust. J. Plant Physiol. 2:311-322.

Jensen, M. E. and J. T. Musick. 1962. Irrigating grain sorghums. Leaflet No. 511 USDA.

Jones, M. M. and H. M. Rawson. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency and osmotic potential in sorghum. Physiol. Plant. 45:103-111.

Kaigama, B. K., I. D. Teare, L. R. Stone, and W. L. Powers. 1977. Root and top growth of irrigated and nonirrigated grain sorghum. Crop Sci. 17:555-559.

Keck, R. W. and J. S. Boyer. 1974. Chloroplast response to low leaf water potentials III. Differing inhibition of electron transport and photophosphorylation. Plant Physiol. 53:474-479.

Kilen, T. C. and R. H. Andrew. 1969. Measurement of drought resistance in corn. Agron. J. 61:669-672.

Krieg, D. R. 1975. Light and water stress effects on seed development of sorghum. 9th Biennial Grain Sorghum Res. and Util. Conf. Lubbock, Texas. p 61.

Krieg, D. R. 1977. Genotypic differences in photosynthetic activity as related to water stress and yield. 10th Biennial Grain Sorghum Res. and Util. Conf. Wichita, Kansas. pp 53-54.

Krishnamurthy, K., A. Bommgowda, M. K. Jaghannath, T. V. Ramachandra Prasad, N. Venugopal, G. Jayaram, and G. Raghunatha. 1975. Impact of moisture stress on the structure of yield in maize (Zea mays L.) I. Effect on grain yield and its components. Mysore J. Agric. Sci. 9:1-6.

Levitt, J. 1980. Responses of Plants to Environmental Stresses I. Chilling, freezing and high temeprature stresses. Acad. Press, New York. 497 p.

Lewis, R. B., E. A. Hiler, and W. R. Jordan. 1974. Susceptibility of grain sorghum to water deficit at three growth stages. Agron. J. 66:589-591.

Ludlow, M. M. and T. T. Ng. 1977. Leaf elongation rate in Panicum maximum var. Trichoglume following removal of water stress. Aust. J. Plant Physiol. 4:263-272.

McCree, K. J. and S. D. Davies. 1974. Effect of water stress and temperature on leaf size and on size and number of epidermal cells in grain sorghum. Crop Sci. 14:751-755.

McWilliams, J. R. and B. Griffing. 1965. Temperature dependent heterosis in maize. Aust. J. Biol. Sci. 18:569-583.

Mirhadi, M. J. and Y. Kobayashi. 1979. The productivity of grain sorghum (Sorghum bicolor) 2. Effects of wilting treatments at different stages of growth on the development, nitrogen uptake, and yield of irrigated grain sorghum. Jpn. J. Crop Sci. 48: 531-542.

Neild, R. E., M. W. Seely, and N. H. Richman. 1978. The computation of agriculturally oriented normals from monthly climatic summaries. Agric. Meteorol. 19:181-187.

Norcio, N. V. 1976. Effects of high temperature and moisture stress on photosynthesis and respiration rate of grain sorghum. Ph. D. Thesis. University of Nebraska, Lincoln. 185 p.

Norcio, N. V. and C. Y. Sullivan. 1976. Stomatal and nonstomatal inhibition of photosynthesis at high temperature. Plant Physiol. 57 (5suppl.):44.

Nour, A. E. M., D. E. Weibel, and G. W. Todd. 1978. Effects of repeated drought periods on the survival of sorghum seedlings. Agron. J. 70:509-510.

Pasternak, D. and G. L. Wilson. 1969. Effect of heat waves on grain sorghum at the stage of head emergence. Aust. J. Agric. Animal Husb. 9:636-638.

Pasternak, D. and G. L. Wilson. 1976. Photosynthesis and transpiration in the heads of droughted grain sorghum. Aust. J. Agric. Animal Husb. 16:272-275.

Panning de Vries, F. T. W., J. M. Witlage, and D. Kremer. 1979. Rates of respiration and of increase in structural dry matter in wheat, rye grass and maize plants in relation to temperature, to water stress and to their sugar content. Ann. Bot. 44:595-609.

Potter, J. R. and J. S. Boyer. 1973. Chloroplast response to low leaf water potentials II. Role of osmotic potential. Plant Physiol. 51:993-997.

Raison, J. K., J. A. Berry, P. A. Armond, and C. S. Pike. 1980. Membrane properties in relation to the adaptation of plants to temperature stress. In N. C. Turner and P. J. Kramer (Eds.). Adaptation of Plants to Water and High Temperature Stress. John Wiley and Sons, New York. pp 261-273.

Redshaw, A. T. and H. Meidner. 1972. Effects of water stress on the resistance to uptake of carbon dioxide in tobacco. J. Expt. Bot. 23:229-240.

Ritchie, J. T. 1974. Atmospheric and soil water influences on the plant water balance. Agric. Meteorol. 14:183-198.

Ross, W. M. 1974. Use of population breeding in sorghum -- problems and progress. In Proc. 28th Ann. Corn Sorghum Res. Conf., Amer. Seed Trade Ass'n., Chicago, Illinois. 1973. pp 30-43.

Ross, W. M. and K. D. Kofoid. 1978. Determining 1000-seed weight in grain sorghum. Crop Sci. 18:507-508.

Salter, P. J. and J. E. Goode. 1967. Crop Responses to Water at Different Stages of Growth. Comm. Wealth Agric. Bur., Furnam Royal, Buks., England. 246 p.

Santarius, K. A. 1967. Assimilation of CO_2, NADP and PGA reduction and ATP synthesis for intact leaf cells in relation to water content. Planta 73:228-242.

Sharp, R. E., O. Osonubi, W. A. Wood, and W. J. Davies. 1979. A simple instrument for measuring leaf extension for grasses, and its application in the study of the effects of water stress in maize and sorghum. Ann. Bot. 44:35-45.

Shearman, L. L., J. D. Eastin, C. Y. Sullivan, and E. J. Kinbacher. 1972. Carbon dioxide exchange in water stressed sorghum. Crop Sci. 12:406-409.

Shipley, J. and C. Regier. 1970. Water response in the production of irrigated grain sorghum, High Plains Texas. Texas Agric. Expt. Stn. Prog. Rep. 2829. 24 p.

Slatyer, R. O. 1967. Plant Water Relationships. Acad. Press, London-New York. 366 p.

Soriano, A. and H. D. Ginzo. 1975. Yield responses of two maize cultivars following short periods of water stress at tasselling. Agric. Meteorol. 15:273-284.

Stickler, F. C., S. Wearden, and A. W. Pauli. 1961. Leaf area determination in grain sorghum. Agron. J. 53:187-188

Stout, D. 1977. Water status and growth of sorghum plants exposed to water stress. 10th Biennial Grain Sorghum Res. and Util. Conf. Wichita, Kansas. p 11.

Stout, D. G., T. Kannangara, and G. M. Simpson. 1978. Drought resistance of Sorghum bicolor 2. Water stress effects on growth. Can. J. Plant Sci. 58:225-233.

Sullivan, C. Y. 1971. Techniques for measuring plant drought stress. In K. L. Larson and J. D. Eastin (Eds.). Drought Injury and Resistance in Crops. CSSA Special Pub. No. 2. Madison, Wisc. pp 1-18.

Sullivan, C. Y. 1972. Meachanisms of heat and drought resistance in grain sorghum and methods of measurement. In N. G. P. Rao and L. R. House (Eds.). Sorghum in Seventies. Oxford and IBH Pub. Co., New Delhi. pp 247-264.

Sullivan, C. Y. and J. D. Eastin. 1969. Effects of heat and drought on the photosynthetic activity of isolated chloroplasts from sorghum, corn and pearl millet. Agron. Abstr. Detroit, p 30.

Sullivan, C. Y. and J. D. Eastin. 1974. Plant physiological responses to water stress. Agric. Meteorol. 14:113-127.

Sullivan, C. Y. and W. M. Ross. 1979. Selecting for drought and heat resistance in sorghum. In H. Mussell and R. C. Staples (Eds.). Stress Physiology in Crop Plants. John Wiley and Sons, New York. pp 263-281.

Sullivan, C. Y., M. D. Clegg, and J. M. Bennett. 1976. A new portable method for measuring photosynthesis. Agron. Abstr. p 77.

Sullivan, C. Y., D. H. Smith, and J. M. Bennett. 1977. Effect of a short duration seedling heat stress on yield of grain sorghum. 10th Biennial Grain Sorghum Res. and Util. Conf. Wichita, Kansas. p 15.

Sung, F. J. M. and D. R. Krieg. 1979. Relative sensitivity of photosynthetic assimilation and translocation of carbon-14 to water stress. Plant Physiol. 64:852-856.

Tollenaar, M., T. B. Daynard, and R. B. Hunter. 1979. Effect of temperature on rate of leaf appearance and flowering in maize. Crop Sci. 19:363-366.

Turner, N. C. and J. E. Begg. 1978. Responses of pasture plants to water deficits. In J. R. Wilson (Ed.). Plant Relations in Pastures. CSIRO:Melbourne. pp 50-66.

Turner, N. C., J. E. Begg, H. M. Rawson, S. D. English, and A. B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits III. Components of leaf water potential, leaf conductance, $^{14}CO_2$ photosynthesis, and adaptation to water deficits. Aust. J. Plant Physiol. 6: 179-194.

Vanderlip, R. L. and H. E. Reeves. 1972. Growth stages of sorghum (Sorghum bicolor L. Moench). Agron. J. 64:13-16

Watts, D. G., J. R. Gilley, and C. Y. Sullivan. 1980. Management of irrigation agriculture with a limited water and energy supply. Final Report to Old West Regional Commission, University of Nebraska and USDA-SEA-AR, Lincoln, Nebraska. 168 p.

Watts, W. R. 1972a. Leaf extension in Zea mays I. Leaf extension and water potential in relation to root zone and air temperature. J. Expt. Bot. 23:704-712.

Watts, W. R. 1972b. Leaf extension in Zea mays II. Leaf extension in response to independent variation of the temperature of the apical meristem, of the air around the leaves and of the root zone. J. Expt. Bot. 23:713-721.

Wien, H. C., E. J. Littleton, and A. Ayanaba. 1979. Drought stress of cowpea and soybean under tropical conditions. In H. Mussell and R. C. Staples (Eds.). Stress Physiology in Crop Plants. John Wiley and Sons, New York. pp 283-301.

Williams, R. F. and R. E. Shapter. 1955. A comparative study of growth and nutrition in barley and rye as affected by low water treatment. Aust. J. Biol. Sci. 8:435.

Williams, T. V., R. S. Snell, and C. E. Cress. 1969. Inheritance of drought tolerance in sweet corn. Crop Sci. 9:19-23

Wilson, D. R., C. H. M. van Bavel, and K. J. McCree. 1980. Carbon balance of water deficient grain sorghum plants. Crop Sci. 20:153-159.

Wilson, J. H. 1968a. Water relations of maize I. Effects of severe soil moisture stress imposed at different stages of growth on grain yields of maize. Rhod. J. Agric. Res. 6:103-105.

Wilson, J. H. 1968b. Water relations of maize II. The effects of nine irrigation regimes on maize. Rhod. J. Agric. Res. 6: 107-108.

Wilson, J. H. H. and J. C. S. Allison. 1978. Effects of water stress on the growth of maize (Zea mays L.). Rhod. J. Agric. Res. 16:175-192.

Womack, D. and R. L. Thurman. 1962. Effects of leaf removal on the grain yield of wheat and oats. Crop Sci. 2:423-426.

APPENDIX

Table A1 Directions for preparing HEDTA-Fe*

To make 1 liter of stock solution:

(1) Place 9.82 g HEDTA (N-(2-Hydroxymethyl)-ethylenediamine tri-acetic acid) in a large beaker.

Add about 200 ml of distilled water
Dissolve by stirring
Add (slowly) 1N NaOH until the HEDTA is completely dissolved (this requires about 120 ml 1N NaOH).

(2) Having the HEDTA completely dissolved, add 13.02 g of ferric nitrate ($Fe(NO_3)_3 \cdot 9H_2O$).

Let the $Fe(NO_3)_3$ completely dissolve by stirring.

NOTE: The color will change from dark pink or red when added to a light pink when fully dissolved.

(3) Having the ferric nitrate fully dissolved:

Place pH electrode in the solution. The solution should at this point be between pH 1 to 2.
Adjust the pH of the solution to pH about 4 by slowly and carefully adding 1N NaOH in a stepwise manner (usually about 80 ml 1N NaOH is required to adjust the pH to about 4).

CAUTION: Addition of NaOH in large quantities or too rapidly will cause the iron to be precipitated out in the form of brown iron oxide. If this happens it is extremely difficult ot get it back into solution.

During the adjustment of the pH the color will change from light pink to dark red.

If the pH goes to 6 or 7 the brown iron oxide precipitate will form.

(4) With the pH adjusted to about 4, bring to volume (one liter) with distilled water.

---

* Personal communication, R.B. Clark.

Table A2 Procedure for heat tolerance test*

(1) Wash leaf discs 4 times with distilled water letting them stand 15 to 20 minutes in the distilled water between washings. Drain off the water.

(2) Let sample stand in water bath at desired temperature (room temperature for controls) for 15 minutes.

(3) Add 20 ml of distilled water and keep at 5 C for 18 to 24 hours.

(4) Shake sample and let stand in water bath at 25 C until temperature has equlibrated.

(5) Read conductivity.

(6) Autoclave at 90 to 100 C for 20 minutes.

(7) Let sample cool down and then let stand in water bath at 25 C until temperature has equlibrated.

(8) Read conductivity.

$$\% \text{ injury} = \left(1 - \frac{1-(T_1/T_2)}{1-(C_1/C_2)} \right) \times 100$$

Where: T_1 is conductivity of treated sample before autoclaving.
T_2 is conductivity of treated sample after autoclaving.
C_1 is conductivity of control sample before autoclaving.
C_2 is conductivity of control sample after autoclaving.

* Personal communication, C. Y. Sullivan.

Table A3 Procedure for desiccation tolerance test*

(1) Wash leaf discs 4 times with distilled water letting them stand 15 to 20 minutes in the distilled water between washings. Drain off the water.
(2) Add 20 ml of desired concentration of osmotic agent (we use polyethylene glycol 600).
(3) Store sample at 5 C for 18 to 24 hours.
(4) Shake sample once by placing the thumb over the test tube and then drain off the osmotic agent.
(5) Add 20 ml of distilled water and again store at 5 C for 18 to 24 hours.
(6) Shake sample and let stand in water bath at 25 C until temperature has equilibrated.
(7) Read conductivity.
(8) Autoclave at 90 to 100 C for 20 minutes.
(9) Let sample cool down and then let stand in water bath at 25 C until temperature has equilibrated.
(10) Read conductivity.
% injury is calculated as in Table A2.

* Personal communication, C. Y. Sullivan.

Table A4. Dry matter (g per plant) at 19 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 5)

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Dry Matter			
1	0	1.42 (100)[1]	0.86 (61)	1.29 (91)	1.19 (84)
	-3	0.86 (61)	0.66 (46)	0.86 (61)	0.79 (56)
	-4.5	0.72 (51)	0.68 (48)	0.73 (51)	0.71 (50)
	mean	1.00 (70)	0.73 (51)	0.96 (68)	
2	-3	1.11 (78)	0.79 (56)	1.08 (76)	0.99 (70)
	-4.5	0.63 (44)	0.71 (50)	0.78 (55)	0.71 (50)
	mean	0.87 (61)	0.75 (53)	0.93 (65)	
3	0	0.95 (67)	0.88 (62)	1.12 (79)	0.98 (69)
	-3	0.80 (56)	0.59 (42)	0.74 (52)	0.71 (50)
	-4.5	0.29 (20)	0.20 (14)	0.36 (25)	0.28 (20)
	mean	0.68 (48)	0.56 (39)	0.74 (52)	
4	-3	0.95 (67)	0.72 (51)	0.79 (56)	0.82 (58)
	-4.5	0.85 (60)	0.62 (44)	0.96 (68)	0.81 (57)
	mean	0.90 (63)	0.67 (47)	0.88 (62)	

Overall Means

Environment	Plant dry matter	Water stress	Plant dry matter	Genotype	Plant dry matter
1	0.90 (63)	0	1.09 (77)	121	0.86 (61)
2	0.85 (60)	-3	0.83 (58)	160	0.67 (47)
3	0.66 (46)	-4.5	0.63 (44)	RS 626	0.87 (61)
4	0.82 (58)				

[1] Numbers in parentheses are dry matter expressed as percentages of genotype 121, water stress 0, environment 1.

Table A5. Dry matter (g per plant) at 27 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 5)

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Dry Matter			
1	0	3.74 (100)[1]	3.15 (84)	3.55 (95)	3.48 (93)
	-3	2.81 (75)	2.01 (54)	2.85 (76)	2.56 (68)
	-4.5	2.24 (60)	1.71 (46)	2.33 (62)	2.09 (56)
	mean	2.93 (78)	2.29 (61)	2.91 (78)	
2	-3	3.14 (84)	2.08 (56)	3.02 (81)	2.75 (74)
	-4.5	2.82 (75)	2.31 (62)	2.80 (75)	2.64 (71)
	mean	2.98 (80)	2.20 (59)	2.91 (78)	
3	0	2.14 (57)	1.71 (46)	2.60 (70)	2.15 (57)
	-3	2.15 (57)	1.29 (34)	2.40 (64)	1.95 (52)
	-4.5	0.99 (26)	0.89 (24)	1.05 (28)	0.98 (26)
	mean	1.76 (47)	1.30 (35)	2.02 (54)	
4	-3	1.98 (53)	1.74 (47)	2.80 (75)	2.17 (58)
	-4.5	1.81 (48)	1.60 (43)	2.31 (62)	1.91 (51)
	mean	1.90 (51)	1.67 (45)	2.56 (68)	

Overall Means

Environment	Plant dry matter	Water stress	Plant dry matter	Genotype	Plant dry matter
1	2.71 (72)	0	2.82 (75)	121	2.38 (64)
2	2.70 (72)	-3	2.36 (63)	160	1.85 (49)
3	1.68 (45)	-4.5	1.91 (51)	RS 626	2.57 (69)
4	2.04 (55)				

[1] Numbers in parentheses are dry matter expressed as percentages of genotype 121, water stress 0, environment 1.

Table A6. Dry matter (g per plant) at 19 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 6)

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Dry Matter			
1	0	0.39 (100)[1]	0.34 (87)	0.65 (167)	0.46 (118)
	-3	0.26 (67)	0.13 (33)	0.21 (54)	0.20 (51)
	-4.5	0.17 (44)	0.11 (28)	0.22 (56)	0.17 (44)
	mean	0.27 (69)	0.19 (49)	0.36 (92)	
2	0	0.14 (36)	0.14 (36)	0.47 (121)	0.25 (64)
	-3	0.22 (56)	0.24 (62)	0.29 (74)	0.25 (64)
	-4.5	0.20 (51)	0.21 (54)	0.28 (72)	0.23 (59)
	mean	0.19 (49)	0.20 (51)	0.35 (90)	
3	0	0.44 (113)	0.51 (131)	1.14 (292)	0.70 (179)
	-3	0.32 (82)	0.20 (51)	0.34 (87)	0.29 (74)
	-4.5	0.30 (77)	0.14 (36)	0.23 (59)	0.22 (56)
	mean	0.35 (90)	0.28 (72)	0.57 (146)	
4	0	0.21 (54)	0.14 (36)	0.36 (92)	0.24 (62)
	-3	0.13 (33)	0.11 (28)	0.26 (67)	0.17 (44)
	-4.5	0.09 (23)	0.09 (23)	0.12 (31)	0.10 (26)
	mean	0.14 (36)	0.11 (28)	0.25 (64)	

Overall Means

Environment	Plant dry matter	Water stress	Plant dry matter	Genotype	Plant dry matter
1	0.28 (72)	0	0.41 (105)	121	0.24 (62)
2	0.24 (62)	-3	0.23 (59)	160	0.20 (51)
3	0.40 (103)	-4.5	0.18 (46)	RS 626	0.38 (97)
4	0.17 (44)				

[1] Numbers in parentheses are dry matter expressed as percentages of genotype 121, water stress 0, environment 1.

Table A7. Dry matter (g per plant) at 26 days after emergence for 3 sorghum genotypes grown under four temperature environments and subjected to various levels of water stress. (Experiment 6)

Environment	Water stress (bars)	Genotype 121	160	RS 626	Mean
		Dry Matter			
1	0	3.06 (100)[1]	1.83 (60)	2.85 (93)	2.58 (84)
	-3	1.00 (33)	1.53 (50)	1.66 (54)	1.40 (46)
	-4.5	0.91 (30)	0.37 (12)	1.62 (53)	0.97 (32)
	mean	1.66 (54)	1.24 (41)	2.04 (67)	
2	0	2.89 (94)	1.58 (52)	3.20 (105)	2.56 (84)
	-3	1.82 (59)	1.53 (50)	2.84 (93)	2.06 (67)
	-4.5	0.78 (25)	1.23 (40)	2.00 (65)	1.34 (44)
	mean	1.83 (60)	1.45 (47)	2.68 (88)	
3	0	3.01 (98)	2.58 (84)	2.66 (87)	2.75 (90)
	-3	1.56 (51)	1.85 (60)	2.82 (92)	2.08 (68)
	-4.5	1.31 (43)	1.00 (33)	1.72 (56)	1.34 (44)
	mean	1.96 (64)	1.81 (59)	2.40 (78)	
4	0	2.31 (75)	2.20 (72)	3.56 (116)	2.69 (88)
	-3	1.85 (60)	1.62 (53)	2.86 (93)	2.11 (69)
	-4.5	0.94 (31)	1.53 (50)	1.22 (40)	1.23 (40)
	mean	1.70 (56)	1.78 (58)	2.55 (83)	

Overall Means

Environment	Plant dry matter	Water stress	Plant dry matter	Genotype	Plant dry matter
1	1.65 (54)	0	2.65 (87)	121	1.79 (58)
2	1.99 (65)	-3	1.91 (62)	160	1.57 (51)
3	2.06 (67)	-4.5	1.22 (40)	RS 626	2.42 (79)
4	2.01 (66)				

[1] Numbers in parentheses are dry matter expressed as percentages of genotype 121, water stress 0, environment 1.

Table A8.1 Mean squares for plant height, leaf dry matter, stem dry matter, and total dry matter of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress (Experiment 1).

Source of variation	df	Plant height	Leaf dry matter	Stem dry matter	Total dry matter
		Mean Squares			
Environment (E)	3	1528.5	11.4*	82.9	883.3
Rep/E	12	358.2	2.6	58.9	275.4
Water stress (W)	3	25679.0**	17.6**	694.1**	10537.6**
E x W	9	495.0**	1.9	55.2	276.9*
W x Rep/E	36	165.6	2.2	33.8	117.5
Genotype (G)	3	1999.5**	251.4**	2854.5**	10338.7**
E x G	9	278.4**	2.6**	13.3	69.8
W x G	9	1774.6**	2.4**	45.9**	508.8**
E x W x G	27	209.7**	0.9	13.1	80.9
G x Rep/(E x W)	144	94.2	0.9	12.2	52.9

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A8.2 Mean squares for panicle weight, number of seeds, and grain yield of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress (Experiment 1).

Source of variation	df	Panicle weight	Number of seeds	Grain yield
		Mean Squares		
Environment (E)	3	470.7	119681.8	231.6
Rep/E	12	62.8	32945.8	22.9
Water stress (W)	3	8246.0**	8770222.9**	5162.6**
E x W	9	163.8**	133708.4*	103.3**
W x Rep/E	36	51.3	52928.9	32.2
Genotype (G)	3	1077.3**	206808.0**	504.1**
E x G	9	34.1	13110.3	18.9
W x G	9	392.7**	214485.3**	229.9**
E x W x G	27	53.2**	59224.8**	40.4**
G x Rep/(E x W)	144	22.0	21797.1	14.7

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A8.3 Mean squares for weight of 1000 seeds of four sorghum hybrids grown under four temperature environments and subjected to two cycles of 0, 4, 8, and 12 days of water stress (Experiment 1).

Source of variation	df	Mean Squares
Environment (E)	3	224.7**
Rep/E	12	33.6
Water stress (W)	3	11.0
E x W	9	17.2
W x Rep/E	36	18.4
Genotype (G)	3	663.6**
E x G	9	21.6
W x G	9	28.1
E x W x G	27	17.7
G x Rep/(E x W)	144	21.2

** Denotes significance at p = .01

Table A9.1 Mean squares for leaf dry matter, stem dry matter, and root dry matter of three sorghum hybrids grown under two temperature environments and subjected to 0, -4, and -6 bars of water stress. (Experiment 3).

Source of variation	df	Leaf dry matter	Stem dry matter	Root dry matter
		Mean Squares		
Environment (E)	1	0.7	318.3*	106.4
Rep/E	10	49.9	271.1	97.1
Water stress (W)	2	30.4*	517.9**	181.8**
E x W	2	1.6	5.3	31.3
W x Rep/E	20	7.7	38.8	21.0
Genotype (G)	2	425.4**	946.4**	624.5**
E x G	2	4.3	31.8	13.8
W x G	4	13.7	33.7	47.1
E x W x G	4	14.5	65.1	8.6
G x Rep/(E x W)	60	13.9	72.5	25.3

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A9.2 Mean squares for panicle weight, number of seeds, weight of 1000 seeds, and grain yield of three sorghum hybrids grown under two temperature environments and subjected to 0, -4, and -6 bars of water stress. (Experiment 3).

Source of variation	df	Panicle weight	Number of seeds	1000-seed weight	Grain yield
		Mean Squares			
Environment (E)	1	104.8	115052.1	88.9*	102.5
Rep/E	10	171.4	253664.5	8.4	101.9
Water stress (W)	2	830.5**	118970.0	97.0**	618.9**
E x W	2	117.0	67364.1	2.6	56.2
W x Rep/E	20	81.4	97004.7	7.3	53.5
Genotype (G)	2	883.1**	343366.8	191.0**	598.2**
E x G	2	21.4	359805.3	38.9**	0.5
W x G	4	355.6*	232338.7	22.0*	253.8*
E x W x G	4	132.6	326316.4	4.8	60.2
G x Rep/(E x W)	60	125.5	130748.9	7.8	77.3

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A10.1 Means squares for top dry matter, root dry matter, and total dry matter of three sorghum hybrids grown under two temperature environments (Experiment 4).

Source of variation	df	Top dry matter	Root dry matter	Total dry matter
		Mean Squares		
Rep	23	32.3	0.46	38.1
Environment (E)	1	4.1	2.35	0.3
Genotype (G)	2	203.1**	2.53**	246.4**
E x G	2	22.6	0.69*	31.1
Error	115	19.2	0.23	22.6

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A10.2 Mean squares for total water use, water use efficiency, and area of the 5th leaf of three sorghum hybrids grown under two temperature environments. (Experiment 4).

Source of variation	df	Total water use	Water use efficiency	Area of the 5th leaf
		Mean Squares		
Rep	23	475656.4	1048.2	64.1
Environment (E)	1	5771205.4	33724.3*	564.1
Genotype (G)	2	1113967.4**	1827.8**	1699.3**
E x G	2	847379.9*	508.7	405.2**
Error	115	220888.0	363.4	57.5

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A11.1 Mean squares for leaf area and dry matter accumulation rates for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 5).

Source of variation	df	Leaf area	Dry matter accumulation rates
		Mean Squares	
Environment (E)	3	965.0	38757.3
Rep/E	8	61.7	3915.0
Water stress (W)	2	6353.5**	20289.6*
E x W	4	506.0**	7973.0
W x Rep/E	12	61.1	4020.0
Genotype (G)	2	2117.7**	33645.9**
E x G	6	194.0	4077.9**
W x G	4	84.7	3222.3*
E x W x G	8	165.3	1521.3
G x Rep/(E x W)	40	103.8	1271.3

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A11.2 Mean squares for net photosynthetic rates measured 14 days after relief of water stress for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 5).

Source of variation	df	Mean Squares
Environment (E)	3	2001.5
Rep/E	8	123.2
Water stress (W)	2	1435.1**
E x W	4	1044.2**
W x Rep/E	12	109.1
Genotype (G)	2	777.6*
E x G	6	199.9
W x G	4	415.8
E x W x G	8	171.1
G x Rep/(E x W)	37	197.0

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A12.1 Mean squares for cumulative leaf area and dry matter accumulation rates of three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 6).

Source of variation	df	Leaf area	Dry matter accumulation rates
		Mean Squares	
Environment (E)	3	4683.8	22404.7*
Rep/E	8	8852.0	10466.4
Water stress (W)	2	80517.5**	261907.7**
E x W	6	3676.4	4265.2
W x Rep/E	16	12199.4	33381.7
Genotype (G)	2	31252.3**	86143.9**
E x G	6	3522.4	6984.4
W x G	4	1321.4	23273.1**
E x W x G	12	6662.5**	12991.9*
G x Rep/(E x W)	48	2142.3	6033.3

* Denotes significance at p = .05
** Denotes significance at p = .01

Table A12.2 Mean squares for net photosynthetic rates measured 13 days after relief of water stress for three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 6).

Source of variation	df	Mean Squares
Environment (E)	3	572.2*
Rep/E	8	177.6
Water stress (W)	2	297.3
E x W	6	127.8
W x Rep/E	15	215.8
Genotype (G)	2	247.0
E x G	6	263.3
W x G	4	132.1
E x W x G	12	243.3
G x Rep/(E x W)	32	299.4

* Denotes significance at p = .05

Table A13 Mean squares for leaf area and total dry matter of three sorghum genotypes grown under four temperature environments and subjected to 0, -3, and -4.5 bars of water stress. (Experiment 7).

Source of variation	df	Area of leaves expanded before imposition of water stress (B)	Area of leaves expanded during the stress period (D)	Ratio B/(B+D)	Total cumulative leaf area	Total dry matter
		Mean Squares				
Environment (E)	3	484.5	6790.0	.00155	210171.2**	21.72**
Rep/E	16	640.6	1175.5	.00107	35652.3	3.60
Water stress (W)	2	595.1	4173.0**	.00152	2140.3	0.23
E x W	4	387.2	3671.6**	.00167	20339.1	1.21
W x Rep/E	24	249.4	485.4	.00072	22639.2	1.59
Genotype (G)	2	31411.9**	37700.1**	.01574**	600662.4**	16.24**
E x G	6	458.2	2177.2**	.00104	12860.5	1.05
W x G	4	207.4	566.8	.00044	4563.6	0.29
E x W x G	8	217.4	1187.2	.00094	11933.0	1.90
G x Rep/(E x W)	80	253.5	697.9	.00050	15483.7	1.18

** Denotes significance at p = .01