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GENETIC ANALYSIS OF DROUGHT TOLERANCE TRAITS IN GRAIN SORGHUM

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ABSTRACT

Sixty four crosses were made among 8 cms lines and 8 restorers of grain sorghum chosen based on their divergence in drought tolerance. The parental lines and their crosses were evaluated in 2 locations under pre-flowering drought stress and non-stress, to study the genotypic variation, interrelationships, heterosis, gene action and heritability of drought tolerance traits based on the combined analysis across locations. The drought tolerant group of genotypes was superior over the susceptible one under water stress for leaf relative water content (RWC) by 59.1 and 66.8%, stay green (SG) by 59.3 and 62.9%, grain yield/plant (GY) by 45.1 and 61.2%, grains/panicle (GPP) by 80.0 and 118.5%, plant dry matter content at flowering (DMT_f) by 37.2 and 58.5%, and at maturity (DMT_m) by 43.5 and 55.4 and leaf area (LA)by 16.9 and 19.8% for parents and F_1's, respectively. Under drought, the strongest significant genetic associations (r_g) were exhibited between GY and each of SG (0.94), DMT_f (0.95) and DMT_m (0.93), suggesting that selection for one or more of these traits could be useful in improving drought tolerance in sorghum. Average positive heterobeltriosis was highest for SG and RWC and lowest for HI. Some crosses under drought showed heterobeltiosis estimates > 75% for GY and > 100% for DMT_f. Both GCA and SCA effects were significant ($p \leq 0.01$); SCA was more important than GCA variance for all traits under drought stress and non-stress, except for LA and HI under non-stress, where the opposite was true. The restorer lines RTX-86, R-89022 and the cms line BTX-631 were the best general combiners under water-stress and non-stress. Dominance was appreciably greater and more affected by environment than additive variance for all cases, except for LA and RWC under drought where additive was larger than dominance. Degree of dominance "a" was over dominance ($a>1.0$) in all cases, except for RWC (no dominance, i.e $a=o$) under drought. Narrow sense heritability estimates were generally higher under non-stress than under water stress and ranged from 12.5% (1000-GW) to 50.5% (LA) under non-stress and from 6.4% (RWC) to 35.4% (LA) under stress.

Key words: *Grain sorghum, Sorghum bicolor, Relative water content (RWC), Stay green (SG), Plant dry matter, Drought tolerance, Inheritance, Heterobeltiosis.*

INTRODUCTION

Grain sorghum (*Sorghum bicolor* L. Moench) is one of the most efficient cereal crops in water utilization. Its ability to withstand water deficits is associated with numerous plant traits that contribute to drought tolerance. However, to date only limited efforts have been made to identify and combine such traits in a breeding program.

Genotype differences in drought tolerance traits have been reported in grain sorghum including leaf relative water content (Wenzel and Berg, 1987, Blum *et al* 1989 and Premachandra *et al* 1995), leaf area (Dhopte *et al 1995* and Al-Naggar *et al* 2002a.), stay green trait (Khizzah and Miller 1992 and Rosenow 1993), dry matter content (Habyarimana *et al* 2004), and grain yield and its components (Al-Naggar *et al* 1999 and 2002a). Thus, producing cultivars of grain sorghum that can yield adequately under water deficit conditions seems possible through selective breeding. Effective improvement in sustaining more productivity under water stress, can occur through breeding most rapidly if physiological processes of drought tolerance are understood.

Physiological processes which are related to drought tolerance, frequently related to leaf water content (Peacock *et al* 1988, Blum *et al* 1989, Premachandra *et al* 1994 and Ashraf and Ahmėd 1998), stay green (Tangpremsri *e, al* 1991, Rosenow 1993 van Oosterom *et al* 1996, El-Bakery *et al* 2003 and Habyarimana *et al* 2004) and accumulated dry matter in plants (Habyarimana *et al* 2004) have all been associated with water use efficiency.

Knowledge of type of gene action and how plant performance under a certain stress is transmitted from the original parents to their hybrids is the first step in designing an efficient breeding program for tolerance to such stress. Little information had been reported in the literature about type of gene action controlling inheritance of grain sorghum traits related to drought and low-N tolerance. Some investigators working on drought tolerance on sorghum reported more importance to additive variance (Jordan *et al* 1983 for epicuticular wax, Kidambi *et al* 1990 for CO_2 assimilation, Basnayake *et al* 1994 for osmotic adjustment and Al-Naggar *et al* 1999 and 2002 b for grain yield, number of grains/panicle, leaf area, leaf temperature, stomatal conductance and carbon exchange rate) while others indicated more importance to dominance variance (Kidambi 1987 for gas exchange processes and Chhina and Phul 1988 for grain yield and its components). Moreover, limited knowledge is available on the values of hybrid vigor of sorghum under drought stress. Therefore the objectives of the present investigation were to study the genotypic differences in traits contributing to pre-flowering drought tolerance in grain sorghum; determine the effect of drought on grain sorghum traits provide information about combining ability, heterosis, type of gene action and heritability for such traits and identify the secondary traits most related to drought tolerance.

MATERIALS AND METHODS

Materials

Forty eight parental lines of grain sorghum (19 B- and 29 R-lines) were screened in a preliminary field experiment in 2002 season at South

Tahrir and Sids for tolerance to drought at pre-flowering stage. In the same season (2002) seeds of A-lines were produced by crossing them with their respective maintainers (B-lines). Out of these forty eight, sixteen lines were selected to be used as parents of this study based on their divergence in absolute and relative yields and visual performances under drought stress and non-stress environments; six parents were tolerant and 10 were sensitive. The six tolerant parental lines consisted of three restorer(R) lines (ICSR-92003, ICSR-93002 and RTx-86-EO-361) and three cytoplasmic male sterile (cms or A) lines (ICSB-91003, BTx-631 and BTx-SPDM-94021). The ten susceptible lines for both drought and low-N stresses consisted of 5 R-lines (ICSR-89022, ICSR-89053, ICSR-90001, ICSR-91022 and RTX-88-V-1080) and 5 A-lines (ICSB-1, ICSB-37, ICSB-47, ICSB-88005 and ICSB-88006). The selected 16 parents were sown on the 25th of June, 2003 at Giza Agric. Res. Station, FCRI, ARC. Each line was grown in two rows of 5 meters long and 70 cm width. The eight restorers (R-lines) were crossed onto the eight A-lines to make 64 F_1 fertile hybrids. The seeds of the 16 parental lines (B and R lines) were also increased in 2003 season by selfing.

Field experiments

In 2004 season, evaluations of 80 genotypes (16 parents and 64 F_1's) were conducted at two locations (Shandaweel and Sids) under two treatments (i.e. non-stress, and pre-flowering drought).Sowing was done on the 3rd of July at Shandaweel and the 25th of June at Sids. A split-block design was used with 3 replications. The two treatments were allotted to the main plots and the genotypes were devoted to sub-plots. Each experimental sub-plot consisted of one row of 5 meters long and 70 cm wide with a total area of 3.5 square meters.Sowing was done in hills of 20 cm apart along the rows.Thinning was done before 1st irrigation (i.e. after 20 days from sowing) and two plants were left in each hill to reach a plant density of 60000 plants/feddan.

Pre-flowering drought stress was conducted, where irrigation was given at planting and 1st irrigation withholden the next two irrigations i.e. for 45 days to impose drought stress for 30 days from panicle initiation to anthesis (at GS2 stage) and then was given until maturity in 15-day intervals. The total number of irrigations for drought treatment was five. The recommended number of irrigations (7) was given to the control. Pest control and other agricultural practices were done for all treatments according to the recommendations of the ARC, Egypt. The soil texture was clayey and clayey-loamy at shandaweel and sids, respectively.

Traits studied

All the following traits were measured as an average of 5 guarded plants taken randomly from each plot: (1) Relative water content (RWC) (%): measured on the 3rd leaf from the top at the end of drought stress (i.e. after 65 days from sowing).The blade of the third leaf was excised after 1300 h of the day 65. The excised leaf was weighed immediately and recorded as fresh weight (FW). Then the cut end of the leaf blade was placed in distilled water in a container and kept under low light conditions in the laboratory. After 5h the leaves were removed, blotted dry, and re-weighed to obtain turgid weight (TW). They were then dried at 70° C for 72 h and reweighed and dry weight (DW) was recorded. Relative water content (RWC) was calculated according to Barrs and Weatherley (1962) as follows: RWC = [(FW–DW)/(TW–DW)] X 100, where FW= fresh weight, DW = dry weight and TW= turgid weight. (2) Leaf area (LA): measured in cm^2 at the time of anthesis on the third leaf from the top and calculated by the following formula proposed by Stickler and Pauli (1961): LA = leaf length X maximum leaf width X 0.747. (3) Stay green (SG): measured as the percentage of green to total leaves at physiological maturity. Physiological maturity was defined as the time at which basal grain in 50 % of panicles attained black layer. (4) 1000 - grain weight (1000GW) (g). (5) Number of grains / panicle (GPP). (6) Grain yield/plant (GY) (g).

At 50 % flowering and physiological maturity stages, five random plants were removed from each sub-plot by cutting at the soil surface. The plants were bulked as one sample per sub-plot and separated into leaf blades and stalks (stalks included leaf sheaths and panicle fractions) at flowering and leaf blades, stalks and panicles (i.e. demarcated by the lowest panicle branch) at physiological maturity (stalks included leaf sheaths only). Samples were dried at 70° C in a forced-air oven for at least 72 hours and weighed. Panicle fractions from each sub-plot were threshed and seed sub-samples were weighed. The following dry matter traits were recorded: (7) Total above ground dry matter/plant (DMT_f) (g) at flowering as follows: DMT_f = stem dry matter + leaves dry matter. (8) Total above ground dry matter/plant (DMT_m) (g) at physiological maturity as follows: DMT_m = stem dry matter + leaves dry matter + grains dry matter (DMG). (9) Harvest index (HI) (%) at physiological maturity stage as follows: HI = (DMG / DMT_m X 100).

Statistical and genetic analyses

Data for all recorded traits, across treatments of each location and combined over the two locations were subjected to a regular analysis of variance of a split block design according to Federer (1963) using the statistical analysis system program (SAS 1989) to estimate mean squares due to genotypes, treatments, locations and all possible interactions among

m. Data of each treatment, separately in each location and combined oss the two locations, were further subjected to a normal analysis of riance of the randomized complete block design. Combined analysis was rformed if the homogeneity test was not significant. Genotypes degrees of edom were partitioned into parents, crosses and parents vs crosses.

Line by tester analysis conducted according to kempthorne (1957) was acticed for each treatment, i.e. non-stress, and drought stress seperately at ch location and combined across the two locations to estimate general and ecific combining ability, type of gene action and their interactions with cations according to Cockerham (1956). Average degree of dominance "a" as calculated from the following equation:- "a" = $(2\,\delta^2_D / \delta^2_A)^{½}$ where δ^2_D dominance variance, δ^2_A= additive variance. The estimates of average gree of dominance "a" were used to determine the type of dominance. arrow sense heritability (h_n^2) were calculated as follows: $^2_n = (\delta^2_A)/(\delta^2_A + \delta^2_D + \delta^2_{Al/L} + \delta^2_{Dl/L} + \delta^2_{e/rL})$ where $\delta^2_A, \delta^2_D, \delta^2_{AL}, \delta^2_{DL}$ nd δ^2_e refer to average additive, dominance additive X locations, ominance X locations and error variances, respectively, and L and r refer to e number of locations and replications, respectively. Genetic correlation $_g$) among studied treatments for each trait (or among traits for each nvironment) were first calculated from variances and covariance as ollows: $r_g = \delta^2_{jk} / (\delta_j\, \delta_k)$; where δ^2_{jk} is the genetic covariance between studied eatments (or between traits) j and k. δ_j and δ_k are the genetic standard eviations of studied treatments (or traits) j and k, respectively.

RESULTS AND DISCUSSION

Analysis of variance (not presented) showed that significant differences ($P \leq 0.01$) existed among the genotypes, parents and F_1 crosses or all studied traits.The differences among drought stress and non-stress reatments were significant ($P \leq 0.01$) for all studied traits. All mean squares lue to genotypes X locations, genotypes X treatments and genotypes X reatments X locations interactions were significant ($P \leq 0.01$) for all studied raits, except grains / panicle for genotypes X locations and genotypes X treatments X locations.Thus, the performance of genotypes varies with locations, and water supply confirming previous results (Saranga *et al* 1990 and Al-Naggar *et al* 1999 and 2002 b).

Mean performance

A comparative summary of means and ranges of all studied traits over all parental lines and hybrids subjected to drought stress and non-stress conditions are presented in Table (1). Results on the effect of each studied abiotic stress (drought and low-N) will be discussed separately.

Effect of drought

Mean grain yield (in dry matter) /plant was significantly reduced b soil moisture stress at pre-flowering (GS2) stage to 82.3 and 83.4% i.e. reduction of 19.7 and 16.6 % over all parents and all F_1 hybrid respectively (Table 1). Previous investigators (Bakheit 1990 and Al-Nagga *et al* 2002a) also reported that soil water stress at pre-flowering stage cause a significant reduction in sorghum grain yield.

Grain yield (GY) under no-stress ranged from 48.2 to 74.3 g/plan with an average of 87.9 g/plant for F_1's (Table 1). While GY under wate stress at GS2 ranged from 40.3 to 61.5 g / plant with an average of 51. g/plant for parents and from 55.1 to 93.4 g / plant with an average of 73. g/plant for hybrids. Both parents and hybrids differed very markedly in thei relative yields (drought tolerance). Such relative yield ranged from 68.9 t 90.9 % for parents and from 70.2 to 92.3 % for hybrids.

Mean 1000-grain weight (1000 GW) under drought was reduced t 81.3 and 84.3% (reduction of 18.7 and 15.7%) for parents and crosses respectively as compared to control. Parents ranged for 1000 GW from 17. to 27.4 g (with an average of 22.9 g) under control and from 15.5 to 22.3 g (with an average of 18.7 g) under drought, while hybrids ranged from 18. to 33.6 g (with an average of 23.0 g) under no- stress and from 16.3 to 27. g (with an average of 19.4 g) under drought stress. Moreover, mean numbe of grains per panicle (GPP) was decreased to 78.0 and 81.5 % (i.e reductio of 22.0 and 18.5 %) when drought was imposed at pre-flowering stage fo parents and hybrids, respectively. For GPP, parents ranged from 1803 t 4067 (with an average of 2829) under no- stress and from 1612 to 345 (with an average of 2207) under drought, while hybrids ranged from 203 to 4690 (with an average of 2961) under control and from 1547 to 405 (with an average of 2412) under drought. Reduction in number of grain per panicle due to water stress was higher than reduction in 1000-grai weight for both parents and hybrids. This result is consistent with tha reported by Bakheit(1990) and Al-Naggar *et al* (1999 and 2002a) wh showed that reductions of sorghum grain yield due to drought stress before anthesis were mainly related to decreases in grain number. In wheat, drought stresses have been found to affect pollen activity, which reduced seed number (Saini and Aspinall, 1981). This effect might also be considered as one of the reasons of reduction in grain number of sorghum subjected to water stress before anthesis.

Table1. Means and ranges (lowest and highest values) of grain sorghum genotypes (G) evaluated under non-stress (NS) and drought stress (S) treatments (T) across two locations.

Parameter	Parental lines			F_1 crosses		
	NS	S	Reduction%	NS	S	Reduction%
1- Leaf relative water content (RWC) (%)						
Mean	50.8	42.3	16.8	77.0	64.0	16.9
Lowest	40.0	31.7	3.8	65.0	49.4	3.3
Highest	67.8	57.0	34.3	92.4	85.3	33.1
LSD$_{05}$	for G= 1.8	for T= 2.6	for GXT = 1.8			
2- Stay green (SG) (%)						
Mean	59.3	45.5	23.3	72.8	62.2	14.6
Lowest	43.7	33.6	10.0	61.0	40.0	4.0
Highest	75.0	63.2	34.2	91.6	77.8	35.7
LSD$_{05}$	for G= 1.94	for T= 4.1	for GXT = 2.8			
3- Leaf area (cm^2)						
Mean	621	524	15.6	755	623	17.4
Lowest	520	422	8.5	630	512	1.9
Highest	730	711	23.5	897	761	33.5
LSD$_{05}$	for G= 8.1	for T= 8.1	for GXT = 7.95			
4- plant dry matter at floweing (DMT_f) (g)						
Mean	93.2	57.3	38.5	125.7	94.2	25.1
Lowest	67.2	48.0	12.4	100.0	72.8	10.4
Highest	115.0	78.8	77.6	150.0	123.8	41.8
LSD$_{05}$	for G= 4.3	for T= 2.5	for GXT = 2.3			
5- Plant dry matter at maturity (DMT_m) (g)						
Mean	110.0	84.4	32.3	141.9	106.9	24.7
Lowest	84.3	64.5	15.6	109.7	81.2	15.2
Highest	136.0	103.0	30.9	180.9	138.7	39.6
LSD$_{05}$	for G= 1.2	for T= 1.9	for GXT = 1.6			
6- Harvest index (HI) (%)						
Mean	57.4	61.4	(-6.9)	62.1	68.7	(-10.6)
Lowest	53.8	58.6	(-21.0)	52.6	61.9	(-24.4)
Highest	61.0	65.6	0.7	68.3	76.2	3.0
LSD$_{05}$	for G= 0.85	for T= 2.9	for GXT = 0.76			
7. Grains/panicle (GPP) (No.)						
Mean	2829	2207	22.0	2961	2412	18.5
Lowest	1803	1612	9.7	2037	1547	6.6
Highest	4067	3450	37.6	4690	4050	30.1
LSD$_{05}$	for G= 37.7	for T= 36.7	for GXT = 32.1			
8. 1000-grain weight (1000GW) (g)						
Mean	22.9	18.7	18.7	23.0	19.4	15.7
Lowest	17.2	15.5	9.1	18.5	16.3	8.0
Highest	27.4	22.3	32.4	33.6	27.6	26.7
LSD$_{05}$	for G= 1.2	for T= 1.5	for GXT = 0.97			
9. Grain yield/plant (GY) (g)						
Mean	62.7	51.6	17.7	87.9	73.3	16.6
Lowest	48.2	40.3	9.1	68.3	55.1	7.7
Highest	74.3	61.5	31.1	115.8	93.4	29.8
LSD$_{05}$	for G= 1.06	for T= 1.2	for GXT = 1.3			

Leaf area (LA) declined significantly when water deficit occurs at GS2 stage. It decreasesd due to water stress to 84.4 and 82.6 % (15.6 and 17.4% reduction) for parental lines and hybrids, respectively. Similar result was reported by Al-Naggar *et al* (2002 a).

The physiological trait relative water content (RWC) reduced significantly as a result of water stress at GS2 stage to 83.2 and 83.1 (16.8 and 16.9 % reduction) for parents and crosses, respectively. Range for RWC trait was 40.0-67.8% with an average of 50.8% (under control) and 31.7-57.0 % with an average of 42.3% (under drought) for parental lines and 65.0-92.4% with an average of 77.0% (under no-stress) and 49.4-85.3 % with an average of 64.0% (under water stress) for crosses. Previous investigators (Peacock *et al* 1988, Premachandra *et al* 1995, Wenzel and Berg 1987 and Ashraf and Ahmed 1998) also reported significant reductions in RWC trait due to soil water deficit before flowering.

Stay green (SG), as an important physiological trait in sorghum decreased significantly as a result of drought at GS2 stage to 76.7 and 85.4 % (by 23.3 and 14.6% reduction) for parental lines and F_1 hybrids, respectively. Less reduction in hybrids might be attributed to hybrid vigour, which helped the hybrids to tolerate water stress in a way better than their parental lines, through keeping higher percentage of leaves green until physiological maturity as compared to the parental lines. Al- Naggar *et al* (1999) observed that pre-flowering water stress significantly reduced No. of green leaves and leaf area in sorghum. They mentioned that the decrease in leaves number and area reflects the increased rate of leaf senescence.

Total plant dry matter which includes leaves and stems at flowering (DMT_f) was decreased because of soil water deficit practiced at GS2 stage to 61.5 and 74.9% for parents and crosses, respectively. Reduction in DMT_f due to drought was more pronounced in parental lines (38.5%) than in F_1 crosses (25.1%). Plant dry matter (which includes leaves, stem and grains) at maturity (DMT_m) was also reduced as a result of water stress at pre-flowering stage to 73.9 and 79.6% (26.1 and 20.4%.reduction) for parents and hybrids, respectively. Reductions in DMT_f and DMT_m due to water stress reported in the present investigation are in agreement with the majority of previous reports on sorghum (Gonzalez-Hernandez *et al* 1992 and Habyarimana *et al* 2004).

Harvest index (HI) increased significantly due to water deficit at GS2 stage by 6.9 and 10.6 % for parents and crosses, respectively (Table 1). Although water stress at pre-flowering stage caused reductions in both grain dry matter (DMG) and total plant dry matter at physiological maturity (DMT_m), the calculated value of HI increased under drought as compared to that under control. These increases in HI might be attributed to the lower reductions in grain dry matter (17.7% for parents and 16.6% for crosses) than reductions in total plant dry matter at maturity (26.1% for parents and

20.4 % for crosses). Increases in HI were also reported by other investigators (Blum *et al* 1992 and Wenzel *et al* 1999).

Genotypic differences

Means of the best and worst parental lines and hybrids under drought stress and non-stress conditions are presented in Table (2). When an advantage in both absolute yield under drought stress and non-stress conditions was taken as an index of drought tolerance, the parental lines ICSR- 93002 and RTX-86 could be regarded as the most drought tolerant lines. Moreover, the crosses ATX-94021 X RTX-86, A-1 X R-89022, ATX-631 X R-89022, A-88006 X RTX-86, A-91003 X RTX-86, A-88006 X R-93002, A-47 X R-90001 and ATX-631 X R-92003 could be considered the most drought tolerant hybrids (Table 2). It is interesting that such lines and hybrids which excelled under drought stress at GS2 excelled also in the potential yield (i.e. under well-watering conditions). On the other hand, the parental lines ICSB-47 and ICSB-88005 could be considered the most drought suceptible lines and the F_1's A-37 X RTX-88, A-88006 X RTX-88, A-88005 X R-91022 and A-37 X R-91022 could be regarded the most drought susceptible hybrids.

Table 2. The best and worst parental lines and F_1 crosses (in a descending order) under non-stress (NS) and water stress (S) conditions across two locations.

Trait	stress	Parental lines		F_1 crosses	
		Best	Worst	Best	Worst
RWC	NS	8,13,7	3,9,2	5×15,6×15,8×15,1×9,7×15	4×10,4×15
	S	10,15,13	2,3,4	7×9,1×9,8×15,5×15,6×15	3×12,5×12
SG	NS	14,8,13	1,3,2	6×15,8×15,5×15,7×15,7×9	4×16,4×10
	S	15,14,6	3,9,4	8×15,6×15,1×9,7×9,5×15	4×16,4×10
LA	NS	15,14,6	11,3,1	1×9,7×9,5×15,6×15,5×14	1×11,8×11
	S	12,6,13	3,11,1	5×15,2×15,1×9,5×14,4×14	7×10,2×16
DMT_f	NS	3,7,14	2,9,4	7×9,6×15,5×15,8×15,1×9	4×16,5×12
	S	15,13,6	4,3,9	1×9,7×9,8×15,5×15,3×11	4×16,6×10
DMT_m	NS	14,13,6	4,9,3	7×9,8×15,3×11,1×9,6×15	4×12,8×16
	S	15,13,6	5,4,3	3×11,1×9,7×9,5×15,8×15	8×16,6×14
HI	NS	8,12,9	7,14,13	6×16,3×15,3×16,2×15,8×16	1×11,7×11
	S	14,9,3	4,12,10	3×16,7×16,6×16,2×15,8×10	6×9,7×10
GPP	NS	4,15,14	2,5,3	7×9,8×15,6×15,1×9,5×14	4×10,5×12
	S	15,14,13	9,4,3	8×15,6×15,7×9,2×10,5×15	4×12,4×10
1000GW	NS	13,15,12	4,9,3	7×9,6×15,8×15,3×13,5×15	4×12,4×10
	S	14,7,12	4,1,3	8×15,6×15,5×15,7×9,1×9	3×10,5×10
GY	NS	15,14,6	4,9,3	7×9,8×15,6×15,1×9,5×15	4×10,2×12
	S	14,15,13	5,4,3	8×15,1×9,7×9,5×15,6×15	4×12,2×12

1= ICSB -1, 2 = ICSB- 37, 3= ICSB-47, 4= ICSB-88005, 5= ICSB-88006, 6= ICSB-91003, 7= BTX-631, 8= BTX-94021, 9= ICSR-89022, 10= ICSR-89053, 11=ICSR-90001, 12= ICSR-91022, 13= ICSR-92003, 14= ICSR-93002, 15= RTX-86, 16= RTX-88

It is interesting to mention that grain yield of F_1 crosses under water stress at GS2 (73.3 g/plant) was generally higher than that of their parental lines (51.6 g/plant). This means that in sorghum the heterozygotes are better in grain yield than homozygotes by 42.0 % under drought stress conditions of this experiment. Therefore, it is recommended that F_1 crosses of grain sorghum are preferred over their parental lines for their yield performance under drought stress conditions at pre-flowering stage. In this respect, Blum *et al* (1992) and Haussmann *et al* (1999) reported that across environments sorghum hybrids outyielded local varieties and / or parental lines.

The same parental lines and F_1 crosses which excelled for grain yield / plant excelled also for number of grains / panicle under both drought and well-watering conditions. In this regard, number of grains/panicle of F_1 crosses under drought at GS2 (2412) was generally greater than that of their parental lines (2207) by about 9.3 %. Haussmann *et al* (1999) mentioned that better performance of hybrids under unvafourable growing conditions may not be caused primarily by greater stress resistance, rather, it could result from the generally higher capacity of hybrids to compensate for, e.g. missing plants or pest attack by increasing the number of kernels per head in the remaining plants .

The tolerant lines to reduction in 1000-grain weight by water deficit, considering their values under drought stress and non-stress conditions were R-91022 and R-93002. On the other hand, the parental lines B-47 and B-88005 showed sensitivity to drought at GS2 stage measured by absolute values for grain weight under both drought and well-irrigation conditions. These sensitive lines to reduction in 1000-grain weight due to drought were also sensitive to reduction in grain yield / plant. The hybrids ATX-94021 X RTX-86, A-91003 X RTX-86, A-88006 X RTX-86, ATX-631 X R-89022, A-1 X R-89022, A-47 X R-92003, A-88006 X R-93002, ATX-631 X R-92003 and A-47 X R-90001 were the most tolerant crosses to the effect of drought stress on 1000-grain weight.

The highest absolute values under drought stress and non-stress environments were exhibited by the parental line B-91003 for leaf area (LA), R-92003 for relative water content (RWC), R-93002 for stay green trait (SG), RTX-86 for plant dry matter at flowering (DMT_f), R-92003 for plant dry matter at maturity (DMT_m), and R-89022 for harvest index (HI). The best F_1 crosses under drought stress and non-stress conditions were A-88006 X RTX-86, for LA, ATX-631 X R-89022, for RWC, ATX-94021 X RTX-86, for SG trait, A-1 X R-89022, for DMT_f, A-47 X R-90001, for DMT_m, and A-47 X R-92003, for HI.

Summarizing the previously mentioned results, it is obvious that the drought tolerance exhibited by different genotypes in terms of grain yield / plant was due to drought tolerance expressed by other characters than yield which were similar in some cases and different in others. In general, the drought tolerance expressed by grain yield/plant in the crosses ATX-94021 X RTX-86, A-1 X R-89022, ATX-631 X R-89022, A-88006 X RTX-86, was due to drought tolerance expressed by number of grains/panicle, 1000-grain weight, leaf area, RWC, SG, DMT_f, DMT_m and HI. Moreover, the drought tolerance expressed by yield in the parental line R-93002 was due to drought tolerance expressed by GPP, SG and PH. The superiority in drought tolerance of the line RTX-86 expressed by yield was associated with drought tolerance expressed by GPP.

Superiority of tolerant over susceptible genotypes

To describe the differences between drought tolerant (T) and susceptible (S) genotypes, data were averaged for the groups of genotypes differing in their tolerance by definition, namely in grain yield under drought stress and non-stress conditions (Table 3). The drought tolerant genotypes used for this description were parental lines R-93002, RTX-86 and R-92003 and hybrids ATX-94021 X RTX-86, A-1 X R-89022, ATX-631 X R-89022, A-88006 X RTX-86 and A-91003 X RTX-86. The drought susceptible genotypes were lines ICSB-47, ICSB- 88005 and ICSB-88006 and hybrids A-37 X RTX-88, A-88006 X RTX-88, A-37 X R-92003, A-88005 X R-91022 and A-37 X R-91022.

Table 3. Mean performance of studied traits averaged over the best (T) and poorest (S) yielding parental lines and F_1 crosses under drought stress across two locations.

	Parental lines			F_1 crosses		
Trait	Tolerant (T)	Suceptible (S)	Superiority %	Tolerant (T)	Suceptible (S)	Superiority %
RWC (%)	55.2	32.6	59.1	88.2	54.9	66.8
SG (%)	59.7	35.4	59.3	77.0	48.5	62.9
LA (cem^2)	572	489	16.9	690	576	19.8
$DMT_f(g)$	68.2	49.7	37.2	120.8	76.2	58.5
$DMT_m(g)$	98.7	68.8	43.5	134.4	86.5	55.4
HI (%)	62.3	61.6	1.1	67.8	65.4	3.7
GPP (No.)	3028	1682	80.0	3753	1718	118.5
1000GW(g)	21.7	16.3	33.1	26.1	16.8	55.4
GY(g)	61.1	42.1	45.1	90.9	56.4	61.2

Grain yield of the drought tolerant (T) was greater than that of the susceptible (S) genotypes by 45.1 and 61.2 % for parental lines and F1 crosses, respectively. Superiority of drought tolerant over susceptible genotypes in grain yield was due to their superiority in the two yield components, i.e number of grains/panicle and 1000-grain weight. Number of grains/panicle of the drought tolerant was greater than that of the susceptible genotypes by 80.0 and 118.5% for parents and crosses, respectively. Moreover, weight of 1000-grains of the drought tolerant genotypes was greater than that of the susceptible ones by 33.1 and 55.4%, for lines and hybrids, respectively. Superiority of T over S groups in grains/panicle was more than two-fold greater than such superiority in 1000-grain weight.

Relative water content (RWC) as an important studied physiological trait for drought tolerance was appreciably greater in the drought tolerant than in the drought susceptible genotypes by 59.1 and 66.8 % for parental lines and F_1 crosses, respectively. Stay green was significantly higher in T than in S by 59.3 and 62.9 % for parents and hybrids, respectively, most likely in accord with the respective differences between T and S in plant water status.

The advantage of drought T over S in relative water content would allow to expect greater plant dry matter at flowering (DMT_f) and at maturity (DMT_m), and harvest index (HI) in T than S genotypes. Consistent to expectation, significant higher values were exhibited in T than in S by 37.2 and 58.5 % for DMT_f, 43.5 and 55.4 % for DMT_m, and 1.1 and 3.7 % for HI for parental lines and F_1 crosses, respectively. Moreover, leaf area (LA) was significantly greater in the drought T than in the susceptible S genotypes by 16.9 and 19.8 % for parental lines and F_1 crosses, respectively. On the average, genotypes classified as the most drought tolerant in terms of grain yield under both drought stress and non-stress conditions had a better plant water status (expressed by RWC trait) and higher values of SG, DMT_f, DMT_m and HI traits, as compared with the most susceptible genotypes.

Differential response of T X T, T X S and S X S crosses

Mean performances of traits were averaged across three groups of F_1 crosses, i.e. T X T, T X S and S X S groups based on grain yield of their parental lines under stress and non-stress conditions (parental tolerance to the drought) and are presented in Table (4). Number of crosses was 9, 30 and 25 for the T X T, T X S and S X S groups, respectively. In general, tolerant X tolerant and tolerant X susceptible crosses had higher values than susceptible X susceptible crosses for all studied traits under both control and stress conditions. Superiority over S X S crosses was generally higher for T X T than that for T X S crosses under stress conditions. The intermediate values of T X S crosses between T X T and S X S crosses indicated that polygenic system controlled the inheritance of studied traits.

Grain yield/plant of drought T X T (80.3 g) and T X S (74.3 g) crosses was greater than that of drought S X S (70.2 g) crosses by 14.4 and 5.8 %, respectively under drought conditions (Table 4). Superiority of drought T X T and T X S over drought S X S genotypes in grain yield was due to their superiority in grains / panicle and 1000-grain weight. Number of grains / panicle of drought T X T (2912) and T X S (2429) was greater than that of

Table 4. Trait differences in $F_1's$ averaged over the TXT, TXS and SXS groups of sorghum under control (non-stress) and drought stress conditions across 2 locations.

Group	No. of $F_1's$	Control	Drought	Control	Drought	Control	Drought
		RWC(%)		SG(%)		LA(cm^2)	
TXT	9	88.5	81.6	91.2	82.1	812	627
TXS	30	80.2	65.9	83.5	80.1	766	604
SXS	25	75.6	58.7	84.2	78.6	720	407
		DMT_f(g)		DMT_m(g)		HI(%)	
TXT	9	131	98	146	110	64.3	69.8
TXS	30	128	92	142	108	62.8	69.2
SXS	25	121	79	140	104	60.5	45.5
		GPP(No.)		1000GW(g)		GY(g)	
TXT	9	3378	2876	24.7	21.2	93.6	88.3
TXS	30	3034	2430	23.3	19.5	89.2	74.3
SXS	25	2724	2269	21.8	18.8	84.1	70.2

drought SXS (2053) genotypes by 41.8 and 18.3%, respectively. Moreover, weight of 1000 grains of drought TXT (21.2g) and T X S (19.47g) genotypes was greater than that of drought S X S (18.81g) genotypes by 12.7 and 3.5 %, respectively. Superiority of drought T X T and T X S over drought S X S groups in grain yield was therefore mostly due to superiority in grains/panicle. Superiority of drought T X T or T X S over S X S in grains/panicle was more than three-fold greater than superiority in 1000-grain weight.

Relative water content (RWC) was greater in drought T X T (81.6%) and T X S (65.9%) than in S X S (58.7%) genotypes under drought by 39.0 and 12.3 %, respectively. The advantage of T X T and T X S over S X S crosses in RWC under water stress conditions would allow to expect superiority in DMT_f, DMT_m and HI. Consistent to expectation, significant higher values were shown in T X T and T X S than in S X S by 24.1 and 16.4 % for DMT_f, 22.9 and 9.2% for DMT_m and 53.4 and 52.1% for HI, respectively, under drought conditions. Moreover, leaf area (LA) was significantly greater in drought T X T (627.3 cm^2) and T X S (604.4 cm^2) than in S X S (407.3 cm^2) crosses by 54.0 and 48.4 %, respectively under water deficit. Stay green showed also higher values for T X T and T X S than S X S crosses under drought stress, but in smaller magnitudes as compared to other traits.

Trait interrelationships

Under water stress in this experiment, stay green trait (SG) has a strong, significant and positive association with each of grain yield/plant, DMT_m, DMT_f and number of grains/panicle (r_g=0.94, 0.93, 0.91 and 0.78, respectively) (Table5). Under normal growing conditions (control), correlations between SG and each of grain yield, DMT_m, DMT_f and relative water content (RWC) were also strong, significant and positive (r_g=0.94, 0.93, 0.86 and 0.90, respectively) (Table 5). This indicates that stay green trait is a good indicator of plant water status, which is reflected on the total plant and grain dry matter characteristics.

Table 5. Genetic correlation coefficients (r_g) between pairs of studied traits of grain sorghum under drought stress (below diagonal) and non-stress (above diagonal) conditions across 2 locations and 80 genotypes (n=480).

Trait	GY	RWC	SG	LA	DMT_f	DMT_m	HI	GPP	1000GW	GY
RWC	0.37		0.90	0.75	0.96	0.90	0.54	0.54	0.51	0.94
SG	0.94	0.37		0.71	0.86	0.93	0.45	0.73	0.71	0.94
LA	0.66	0.21	0.60		0.26	0.59	0.48	0.48	0.34	0.71
DMT_f	0.95	0.37	0.91	0.67		0.33	ns	ns	0.17	0.36
DMT_m	0.93	0.39	0.93	0.58	0.89		ns	0.61	0.70	0.92
HI	0.63	0.22	0.65	0.53	0.61	0.32		0.34	ns	0.48
GPP	0.58	0.31	0.78	0.36	0.53	0.59	0.25		0.66	0.69
1000GW	0.66	0.24	0.61	0.42	0.57	0.76	ns	0.56		0.63

All numerical values are highly significant, but ns indicates non-significance

These results are in agreement with those reported by McBee *et al* (1983), Van Oosterom *et al* (1996), Borrell *et al* (2000), and El-Bakry *et al* (2003). Borrell *et al* (2000) reported that under terminal water deficit, grain yield was correlated positively with retention of green leaf area at maturity (GLAM), known as stay green (r=0.75**) and negatively with rate of leaf senecence (r=-0.74**). They also concluded that the stay green trait did not constrain yield in the well-watered control. Xu *et al* (2000) indicated that visual stay green ratings were reliable indication of leaf senescence and should be useful to breeders evaluating segregating generation progenies or among genotypes of grain sorghum for post-flowering drought tolerance.

Significant and positive correlations were found in this study between total plant dry matter at maturity (DMT_m) and each of grain yield/plant (r_g=0.93 and 0.91), 1000-grain weight (r_g=0.76 and 0.70) and grains / panicle (r_g=0.59 and 0.61), under drought stress and non-stress, respectively (Table 5). Grain yield in sorghum was found to be associated with high above-ground dry matter (Haussmann *et al* 1999). Habyarimana *et al* (2004) stated that differences in biomass potential contributed to dry matter yield differences under water limiting conditions. Tangpremsri *et al* (1991) stated that total dry matter was well related to osmotic adjustment during grain filling.

Relative water content (RWC) under control conditions exhibited significant, positive and high-magnitude genetic correlation coefficients with grain yield/plant (0.94), DMT_f (0.96). LA (0.75), HI (0.54), grains/panicle (0.54) and 1000 grain weight (0.51) (Table 5). However, under drought conditions, RWC was low in magnitude, but had highly significant positive correlations with SG, grain yield, DMT$_f$, grains/panicle, 1000-grain weight (r_g=0.37, 0.37, 0.39, 0.31 and 0.24, respectively) (Table 5). Wenzel and Berg (1987) reported a significant correlation (r=0.89) between excised leaf water retention capability (ELWRC) and yield potential of grain sorghum genotypes under drought conditions. They concluded that ELWRC was a satisfactory screening technique for drought resistance of the sorghum genotypes. Xu *et al* (2000) in grain sorghum reported that RWC in top leaves of the stay green lines was about 81 %, higher than non-stay green lines (38%), indicating that the stay green lines kept the stalk transporting system functioning under severe drought conditions.

The strongest association (>0.92) of grain yield/plant under water stress in this study was with each of SG, DMT$_f$ and DMT$_m$ (physiological traits). Moreover, under control conditions, the strongest association (> 0.92) of grain yield was with each of SG, DMT$_m$ and RWC (also physiological traits). This suggested that selection for one or more of these traits under drought conditions could be considered useful for increasing grain yield under drought stress.

Correlation coefficients between means under drought stress and those under non-stress conditions for each trait were very high in magnitude, positive and highly significant for grain yield/plant (0.95), stay green trait (0.93) and total DM at maturity (0.92). This suggested that selection under non-stress would be efficient for increasing the same traits under drought stress conditions if the heritability in narrow sense of these traits under both environments was high.

Heterosis

The contrast between parents and crosses was significant ($P \leq 0.01$) under studied drought stress and non- stress treatments for all studied traits, suggesting significant heterotic effects. The heterosis X location interaction was significant ($P \leq 0.01$) for most studied traits, suggesting that the expression of heterosis was not stable across the two locations for these traits. The exceptions were DMT$_m$ under no-stress and grains/panicle, DMT$_m$ and HI under drought, where heterosis was stable across locations. The expression of useful heterosis (heterobeltiosis) averaged across locations differed for the different studied traits (Table 6).

Average positive heterobeltiosis across all crosses reached its maximum positive value in stay green trait (87.1 and 79.7 %) followed by RWC (78.8 and 74.6 %), DMT$_f$ (34.2 and 31.0), grain yield/plant (30.4, 31.0 and 29.5 %) and NUE$_e$ (29.9, 31.4 and 30.8 %) under control and drought, respectively (Table 6). The lowest positive average heterobeltiosis was exhibited by harvest index (6.5 and 10.7 under no-stress and drought stress,

Table 6. Heterobeltiosis (%) estimates (average, the lowest and highest values) and the best and worst sorghum crosses in heterosis under non-stress (NS) and stress (S) conditions across 2 locations (2004 season).

Trait	Stress	Heterobeltiosis			Best	Worst
		Average	Lowest	Highest	F_1's	F_1
RWC	NS	78.8	24.9	89.8	3x11,3x9,4x9,2x11,1x16	5x12
	S	74.6	21.5	80.3	7x9,2x11,1x9,1x11,1x16	8x11
SG	NS	87.1	28.9	91.7	1x16,3x9,3x11,2x11,7x9	4x15
	S	79.7	22.9	88.6	3x11,7x9,1x9,1x12,2x11	7x14
LA	NS	14.6	4.5	44.6	1x9,7x9,1x16,4x11,3x11	2x15
	S	11.9	(-23.2)	45.4	1x16,3x11,4x11,5x15,1x9	6x9
DMT_f	NS	34.2	(-10.8)	88.4	2x9,1x9,4x9,8x9,1x16	7x11
	S	54.5	11.8	129.2	2x9,1x9,4x9,8x9,1x16	1x15
DMT_m	NS	19.8	(-13.3)	70.7	2x9,3x9,1x9,4x9,3x11	8x14
	S	17.8	(-11.0)	82.2	1x9,3x11,2x9,2x11,1x16	6x14
HI	NS	6.5	(-10.8)	22.0	6x16,7x14,3x12,6x13,3x15	2x13
	S	10.7	(-4.1)	22.0	7x16,6x16,3x16,1x13,4x15	2x14
GPP	NS	17.6	(-32.0)	70.4	7x9,1x9,4x10,4x12,4x16	4x15
	S	15.1	(-31.9)	77.3	2x10,1x9,2x16,7x9,3x11	2x13
1000GW	NS	14.7	(-0.4)	36.6	7x9,8x13,4x12,5x12,1x15	4x15
	S	9.3	(-13.2)	42.9	1x9,1x16,6x16,8x15,6x14	2x13
GY	NS	30.3	(-2.4)	84.2	1x9,3x9,2x9,7x9,1x16	4x12
	S	31.0	7.4	93.6	1x16,1x12,2x9,3x11,2x11	2x13

respectively). In general, average positive heterobeltiosis was higher under drought stress (for grain yield/plant, DMT_f and HI) than under non-stress conditions. However, for LA, RWC and SG, the average positive heterobeltiosis was higher under non-stress than under drought. The highest estimates of heterobeltiosis reached maximum in some crosses for grain yield/plant (more than 75%) and DMT_f (more than 100%) under drought conditions.

Positive heterobeltiosis estimates were obtained under drought conditions for all studied characters, (Table 6). The highest heterobeltiosis estimates for grain yield under drought were shown by the A-1 X R-89022 (93.6%) followed by A-1 X RTX-88 (77.6 %), A-1 X R-91022 (77.1 %), A-37 X R-89022 (75.8%) and A-47 X R-90001 (67.3 %). The majority of these crosses showed also the highest estimates of heterobeltiosis for grain yield under non-stress conditions. These crosses were also superior in heterobeltiosis under drought for grains/panicle and / or 1000-grain weight. Moreover, the majority of these crosses exhibited the highest estimates of heterobeltiosis under drought for stay green, DMT_m, DMT_f and RWC traits, i.e. for important physiological traits in drought tolerance.

Under drought stress conditions, ranges of heterobeltiosis differed in different characters. The cross A-1 X R-89022 showed the highest heterobeltiosis estimates in grain yield (93.6 %), leaf area (33.0 %), RWC

(72.1 %), SG (82.6 %), DMT_f (129.2 %) and DMT_m (82.2 %) under drought.

The existence of heterosis for different characters in grain sorghum crosses under either control or soil moisture stress had been demonstrated by several authors. Quinby (1963) measured either the third or the fourth leaf blade from the top of the plant and found that leaf blades of hybrids were larger than those of parents. They also reported that greater leaf blade of hybrids was not a major cause of greater grain yield. Van Oosterom *et al* (1996) reported that the expression of heterosis for non-senescence as related to the stay-green trait was stable across experiments. Patanothai and Atkins (1971) showed that the head weight of the hybrids was much greater than their parents and they ascribed this phenomenon to the fact that growth is exponential and that the limit of the stover production is determined in the first one third of the life cycle and the limit of grain production is in the second third of the life cycle. Seeds produced by sorghum hybrids are frequently heavier than average seed weight of the parents (Kambal and Webster 1966). Blum *et al* (1992) found that sorghum hybrids subjected to drought stress produced more grain compared with open-pollinated cultivars. Sinha and Khanna (1975) noted evidence on heterosis in photosynthesis in hybrids over their parents. Blum *et al* (1990) reported that significant heterosis for biomass, grain yield per plant and grain number per panicle; no heterosis occurred for harvest index, indicating that heterosis in grain yield was due to heterosis in biomass. On the contrary, Kirby and Atkins (1968) found that seed weight of hybrids did not differ significantly from parents.

Combining ability

Mean squares due to males and females in their respective crosses were highly significant for all studied traits under control and drought (data not presented). This indicated that estimates of GCA effects were insignificant for both parental males and females for all traits. Variation due to male X female interaction was also highly significant for all studied traits under optimal and drought conditions, except for LA under control which was insignificant. This suggests that SCA effects were significant at the 0.01 level for studied traits under optimal, and drought. Similarly, highly significant mean squares due to female X location, male X location and female X male X location interactions were detected for all traits under all studied treatments, except leaf area and grains/panicle under control and harvest index and grains/panicle under drought for the three interaction components, which were insignificant. This indicates that GCA effects of both females and males and SCA effects of females X males interacted differently with locations in the majority of cases under the two studied treatments.

Contribution of the variation due to females, males and females X males to the total variation for studied traits under optimal and drought conditions is presented in Table (7). In general, contribution of the variation due to females X males interaction (SCA variance) to the total variation was greater than 50 % (i.e. greater than GCA variance) for 7 traits out of 9 under control (RWC, SG, grains/panicle, 1000-GW, grain yield/plant, DMT_f, DMT_m) and for all traits under drought, suggesting that SCA variance was more important than GCA variance in the inheritance of these characters. For two traits (LA, HI) under control, females X males interaction variance was less than 50 % of the total variance, suggesting that SCA variance was less important than GCA variance in the inheritance of these characters under non-stress conditions.

Table 7. Proportional contribution (%) of females (F), Males (M) and F X M to total variance for studied traits under control and drought environments across 2 locations

Trait	Control			Drought		
	F	M	FXM	F	M	FXM
RWC	12.0	26.8	61.2	10.2	23.2	66.6
SG	14.5	25.3	60.2	13.8	14.8	71.4
LA	14.5	44.8	40.6	7.9	39.7	52.4
DMT_f	15.2	23.3	61.8	11.7	18.2	70.1
DMT_m	11.4	30.5	58.1	11.2	18.6	70.2
HI	9.8	53.0	37.2	10.9	24.3	64.8
GPP	15.0	23.5	61.5	8.7	15.5	75.8
1000GW	9.8	22.3	67.9	7.4	20.9	71.7
GY	16.1	22.4	61.5	12.1	17.5	70.4

Contribution of variation due to males to the total variation was greater than the contribution of the variation due to females for all studied traits under control, indicating that under control most of the total GCA variance was due to males GCA variance for these traits. Under water stress, the contribution of variation due to males to the total variation was greater than the contribution of variation due to females for all studied 12 traits, except days to flowering, which indicated that both females and males showed equal share in total GCA variance.

General combining ability effects

The best parental lines for GCA effects of studied traits under optimal and drought conditions are given in Table (8). The restorer line RTX-86 (drought tolerant) was the best general combiner for increasing performance of its hybrid combinations regarding grain yield/plant, GPP, 1000-GW, LA, RWC, SG, DMT_f and DMT_m under optimal, and drought conditions. The restorer line R-89022 showed also the best general

Table 8. The best and worst sorghum parental lines (males and females) for general combining ability ($\hat{g}_i$) and females X males crosses for specific combining ability ($\hat{S}_{ij}$) effects under non-stress and drought stress across 2 locations.

Trait stress		Females		Males		Females x Males	
		Best $\hat{g}_{i(f)}$	Worst $\hat{g}_{i(f)}$	Best $\hat{g}_{i(m)}$	Worst $\hat{g}_{i(m)}$	Best $\hat{S}_{ij}$	Worst $\hat{S}_{ij}$
RWC	NS	7,3,1	4,2,5	15,19,13	10,12,16	5×14,5×15,1×9,7×9,4×11	1×15
	S	6,7,1	4,2,5	15,9,11	12,10,16	7×9,1×9,5×15,3×11,5×14	1×15
SG	NS	7,3,6	4,2,5	15,19,13	10,12,16	5×14,8×15,3×13,1×16,1×9	1×15
	S	7,1,3	4,2,5	15,9,11	10,16,12	5×14,8×10,2×11,6×16,4×11	1×15
LA	NS	6,5,7	3,2,8	15,14,13	10,16,11	1×9,7×9,4×11,5×11,3×13	8×9
	S	1,5,4	8,2,3	15,14,13	10,12,11	1×9,3×11,6×16,4×11,8×12	7×11
DMT_f	NS	3,7,6	4,2,5	15,9,13	10,12,16	5×14,4×11,1×16,6×16,8×10	7×11
	S	1,7,3	4,2,5	15,9,11	10,16,12	2×11,5×14,6×16,8×10,3×11	1×15
DMT_m	NS	8,3,6	2,5,4	14,16,15	11,10,12	5×14,1×16,8×15,4×11,8×10	1×15
	S	1,6,8	2,5,3	16,15,14	10,11,9	5×14,2×11,3×11,5×15,6×16	1×15
HI	NS	8,6,3	2,5,4	14,16,15	11,10,12	2×15,6×12,6×13,7×9,3×15	2×13
	S	1,6,8	2,5,3	16,15,14	10,11,9	8×10,3×16,2×15,2×10,1×13	6×9
GPP	NS	7,3,1	4,2,5	15,9,14	12,10,16	5×14,7×9,4×11,8×15,1×16	7×11
	S	7,1,8	4,2,5	15,9,14	10,12,16	2×10,5×14,8×15,6×15,7×9	1×15
1000GW	NS	7,3,6	4,2,5	15,9,13	10,16,12	7×9,5×14,6×15,3×13,1×16	1×15
	S	7,1,8	4,2,5	15,9,13	10,14,16	8×15,3×13,7×9,5×15,6×15	1×15
GY	NS	7,3,1	4,2,5	9,15,11	10,12,16	5×14,4×11,7×9,8×10,1×16	1×15
	S	1,7,3	4,2,5	15,9,11	10,12,16	8×10,5×14,2×11,6×16,8×12	1×15

1= ICSB -1, 2 = ICSB- 37, 3= ICSB-47, 4= ICSB-88005, 5= ICSB-88006, 6= ICSB-91003, 7= BTX-631, 8= BTX-94021, 9= ICSR-89022, 10= ICSR-89053, 11=ICSR-90001, 12= ICSR-91022, 13= ICSR-92003, 14= ICSR-93002, 15= RTX-86, 16= RTX-88

combiner for grain yield/plant, GPP, 1000 GW, DMT_f, SG, RWC, and HI, under the two treatments (optimal and drought). The restorer line R-90001 showed superiority as the best general combiner for increasing HI and grain yield / plant under control and drought, RWS, SG and DMT_f under drought. The cms line BTX-631 (drought tolerant) was the best general combiner for GY, GPP, 1000 GW, SG, DMT_f, under stress and non-stress conditions and RWC under drought. The cms line B-1 was also the best general combiner for grain yield/plant, under the two treatments, LA, SG, GPP, 1000 GW, DMT_m, RWC, DMT_m and HI under drought. The cms line B-47 was the best general combiner for grain yield/plant, SG and DMT_f under optimal, and drought and RWC, GPP and 1000GW under control.

It is worthy to note that the best two general combiners in this study (the best restorer RTX-86 and the best cms line BTX-631) are tolerant to drought. These two lines could be recommended to sorghum breeders as high-yielding genotypes *per se* and as parents in hybrid combinations under drought stress conditions.

Specific combining ability effects

The best crosses for SCA effects of studied traits under optimal and drought are presented in Table (8). Under non-stress conditions, the highest positive estimates of SCA effects were exhibited by the cross A-88006 X R-93002 for grain yield / plant, GPP, DMT_f, DMT_m, RWC, SG, A-1 X R-89022 for LA, ATX-631 X R-89022 for 1000-GW and A-37 X RTX-86 for HI. Under drought conditions, the highest positive SCA effects were exhibited by the cross ATX-94021 X R-89053 for grain yield/plant and HI, A-88006 X R-93002 for SG and DMT_m, A -1 X R-89022 for LA, ATX-631 X R-89022 for RWC, A-37 X R-89053 for GPP, ATX-94021 X RTX-86 for 1000GW and A-37 X R-90001 for DMT_f.

For grain yield/plant, the highest positive SCA effects were shown by the crosses ATX-94021 X R-89053 (T X S), A-88006 X R-93002 (S X T), A-91003 X RTX-88 (T X S) under optimal, and drought, A-37 X R-90001 (S X S) and A-91003 X R-91022 (T X S) under drought conditions. The hybrid A-88006 X R-93002 (S X T for drought stress) had the highest positive SCA effects for maximum number of traits under stress and non-stress treatments (grain yield/plant, GPP, 1000 GW, SG, RWC, DMT_f and DMT_m). The cross ATX-94021 X R-89053 (T X S for drought stress) showed the highest positive SCA effects for 4 traits (grain yield /plant, DMT_f, DMT_m and SG) under both treatments. Moreover, the cross A-91003 X RTX-88 (T X S) exhibited the highest positive SCA effects for 5 traits under both treatments (grain yield/plant, DMT_f, HI, LA, SG). However, the cross A-37 X R-90001 (S X S) showed the highest positive SCA effects under drought but not under optimal conditions for grain yield/plant, SG, DMT_f, DMT_m. High SCA effects of this cross may be attributed to the high GCA effects of one of its parents (R-90001).

Genetic variance and degree of dominance

Genetic variance components estimates were appreciably larger for dominance (δ^2_D) than for additive (δ^2_A) variance for most studied traits under control and drought (Table 9). Dominance was larger than additive variance for RWC, SG, GPP, 1000GW, grain yield/plant, DMT_f, DMT_m and HI, under control and LA, SG, GPP, 1000GW, grain yield/plant, DMT_f, DMT_m, and HI under drought. On the other hand, the magnitude of additive (δ^2_A) was larger than that of dominance (δ^2_D) variance in LA, under control, and RWC under drought.

Moreover, the magnitude of interaction for δ^2_D X locations was markedly higher than that for $\delta^2_{A\,X}$ locations for all studied traits under stress and non-stress treatments, except for GPP and DMT_f under control where $\delta^2_{A\,X}$ locations was higher than $\delta^2_{D\,X}$ locations. This indicates that for most traits, dominance type of gene action was more affected by environment than additive type. However, for the exceptions, non-additive

Table 9. Estimates of additive (δ^2_A), dominance (δ^2_D), additive x location (δ^2_{AL}) and dominance x location (δ^2_{DL}) interaction variance, degree of dominance "a" and heritability in narrow-sense (h^2_n) for studied sorghum traits under drought stress (S) and non-stress (NS) conditions across 2 locations.

Trait	stress	δ^2_A	δ^2_D	δ^2_{AL}	δ^2_{DL}	"a"	h^2_n
RWC	NS	12.05	38.92	-	-	2.54	23.3
	S	11.21	(-104.2)	-	-	0.00	6.4
SG	NS	15.10	45.10	-	-	2.44	24.8
	S	8.54	83.33	-	-	4.42	9.2
LA	NS	2145	2087	(-3.46)	(-18.3)	1.39	50.2
	S	1256	2038	24.8	535	1.80	35.4
DMT_f	NS	187.6	200.8	13.92	4.4	1.46	46.8
	S	23.7	190.4	0.7	8.2	4.00	10.7
DMT_m	NS	68.0	97.8	2.9	11.1	1.70	39.0
	S	26.7	210.7	0.1	14.5	3.97	10.9
HI	NS	6.43	15.32	0.8	3.3	2.18	26.8
	S	2.35	5.83	(-0.7)	(-3.3)	2.23	15.5
GPP	NS	101315	340887	12	(-621)	2.59	22.9
	S	64511	297203	15	20	3.03	17.9
1000GW	NS	1.69	10.42	0.42	1.77	3.51	12.5
	S	0.71	7.53	0.16	1.27	4.61	7.8
GY	NS	33.85	112.3	0.58	3.93	2.57	22.9
	S	14.79	123.7	(-0.04)	2.33	4.09	10.5

component was less affected by location than the additive component i.e. for DMT_f and GPP under control.

Similar results were obitained by Kidambi (1987) and Al-Naggar *et al* (1999) who realized the importance of non-additive genetic variance in the inheritance of gas exchange processes under water stress environments. They concluded that breeding programs which exploit the heterozygosity would lead to improvements in the physiological processes and increased water use efficiency. These results were in agreement with those obtained by Chhina and Phul (1988) who reported that non-additive gene action was thought to be of major importance in the inheritance of grain yield and its components under irrigated and limited irrigation environments. Also, Patel and Desai (1990) had similar conclusion (i.e. importance of non-additive gene effects) for yield and seven yield components in crosses among five cms lines and 22 males. While, Mishra *et al* (1992) found that harvest index, grain yield and its related characters were governed by both additive and non-additive gene effects. On the other hand, Laosuwan and Atkins (1977) found that additive gene effects of the R-lines accounted for the largest portion of the variation expressed for grain yield, heads/plant; 100-seed weight and seeds/head. These results were consistent with those obtained by

Pathak and Sanghi (1992) who found that additive variance was more important than dominance variance in controlling the majority of leaf traits in forage sorghum.

Degree of dominance "a" was overdominance (a > 1.0) for all studied traits under both stress and non-stress condations, except for RWC (no dominance i.e. a = 0) under drought (Table 9).

Heritability

Narrow-sense heritability (Table 9) ranged from 12.5% (for 1000GW) to 50.5% (for LA) under control, and from 6.4 % (RWC) to 35.4% (AL) under drought. Narrow-sense heritability for grain yield/plant was of low magnitude (22.9 %) under control and of very low magnitude under drought (10.5%). Low heritability estimates in narrow-sense are generally due to non-uniform testing conditions, small genotypic (additive) variance or large genotype X environment interaction variances (Smith *et al* 1990). Even in a situation where all moisture is provided by controlled irrigation, uniform application of small amounts of water can be difficult, resulting in non-uniform test conditions and consequently high experimental error (Calhoun *et al* 1994). Also, deficient moisture can execrate other sources of experimental error such as soil heterogeneity.

The largest h^2_n was shown by 3 traits under control (LA, DMT_f and DMT_m) and one trait under drought (LA). In general, heritability estimates in the narrow-sense decreased under stress compared to non-stress for all studied traits. Similar to our results, some researchers reported a decrease in heritability under stressed environments (Frey 1964 and Asay and Johnson 1990).

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التحليل الوراثي لصفات تحمل الإجهاد المائي في الذرة الرفيعة للحبوب

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تم تهجين ٨سلالات عقيمة الذكر سيتوبلازميا و٨ سلالات معيدة للخصوبة من الذرة الرفيعة للحبوب لانتاج ٦٤هجين، وكانت الآباء مختارة بحيث تختلف في تحملها للاجهاد المائي، تم تقييم ٨٠تركيب وراثي (١٦ آباء و٦٤ هجين) في موقعين (شندويل وسدس) تحت ظروف الاجهاد وعدم الاجهاد المائي في مرحلة ماقبل التزهير لدراسة التباينات بين التراكيب الوراثية والارتباطات وقوة الهجين ونوع فعل الجين وكفاءة التوريث لصفات تحمل الجفاف بالاعتماد على تحليل البيانات عبر الموقعين. تم عمل معاملة الاجهاد المائي عن طريق منع الريتين التاليتين لرية المحاياة واعطاء الريات الأخرى. عند مقارنة مجموعتي التراكيب الوراثية (المتحملة للجفاف والحساسة) تحت الاجهاد المائي أظهرت التراكيب المتحملة قيم أعلى لصفات محتوى الماء النسبي بـ ٥٩,١ ، ٦٦,٨% والبقاء الأخضر بـ ٥٩,٣ ، ٦٢,٩% والمحصول بـ ٤٥,١، ٦١,٢% وعدد الحبوب بالقنديل بـ

٨٠,٠، ١١٨,٥%، ومحتوى الماء الجافة عند التزهير بـ ٣٧,٢، ٥٨,٢% وعند النضج بـ ٤٣,٥، ٥٥,٤% ومساحة الورقة بـ ١٦,٩، ١٩,٨% عن التراكيب الحساسة بالنسبة للآباء والهجن، على الترتيب. ظهرت أقوى الارتباطات الوراثية (r_g) تحت الاجهاد المائى بين محصول الحبوب وكل من البقاء الأخضر (٠,٩٤) ومحتوى المادة الجافة عند التزهير (٠,٩٥) وعند النضج (٠,٩٣)، مما يقترح أن الانتخاب لصفة أو أكثر من هذه الصفات قد يكون نافعاً فى تحسين تحمل الاجهاد المائى فى الذرة الرفيعة. وكان أعلى متوسط لقوة الهجين النافعة (بالنسبة للأب الأحسن) فى صفتى البقاء الاخضر ومحتوى الماء النسبى للورقة وأقل متوسط لدليل الحصاد. أظهرت بعض الهجن تحت الجفاف قوة هجين نافعة أكبر من 75% لمحصول الحبوب وأكبر من ١٠٠٪ لمحتوى المادة الجافة عند التزهير، كانت كلا من تأثيرات القدرة العامة والخاصة على الائتلاف عالية المعنوية، وكان تباين القدرة الخاصة أكثر أهمية من تباين القدرة العامة على الائتلاف فى كل الحالات ماعدا صفتى مساحة الورقة ودليل الحصاد تحت ظروف الاجهاد المائى، حيث كان العكس صحيحاً. كانت السلالتين المعيدتين للخصب RTX-86 ، R-89022 والسلالة عقيمة الذكر BTX-631 الأحسن فى القدرة العامة على الائتلاف تحت كلا من الاجهاد وعدم الاجهاد المائى. كان تباين السيادة أكبر كثيراً من التباين المضيف فى كل الحالات ماعدا صفتى مساحة الورقة والمحتوى النسبى للماء بالورقة تحت ظروف الاجهاد المائى حيث كان العكس صحيحاً، كان تباين السيادة أكثر تأثراً بالبيئة من التباين المضيف فى معظم الصفات، كانت درجة السيادة هى السيادة الفائقة فى كل الحالات، ماعدا صفة محتوى الماء النسبى بالورقة حيث أظهرت عدم وجود سيادة تحت ظروف الاجهاد المائى، كانت قيم كفاءة التوريث الخاصة أعلا بصفة عامة تحت ظروف عدم الاجهاد عن الاجهاد المائى وتراوحت بين ١٢,٥% (الوزن ١٠٠٠ حبة) إلى ٥٠,٥% (لمساحة الورقة) تحت ظروف عدم الاجهاد ومن ٦,٤% (لمحتوى الماء النسبى) إلى ٣٥,٤% (لمساحة الورقة) تحت الاجهاد المائى.