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Hybrid performance of sorghum and its relationship to morphological and physiological traits under variable drought stress in Kenya

B. I. G. HAUSSMANN[1], A. B. OBILANA[2], A. BLUM[3], P. O. AYIECHO[4], W. SCHIPPRACK[5] and H. H. GEIGER[1,6]

[1] Institute of Plant Breeding, Seed Science, and Population Genetics, University of Hohenheim, D–70593 Stuttgart, Germany; [2] ICRISAT, PO Box 776, Bulawayo, Zimbabwe; [3] Agricultural Research Organization, The Volcani Center, POB 6, Bet Dagan, Israel; [4] Department of Crop Science, University of Nairobi, PO Box 30197, Nairobi, Kenya; [5] Nordsaat, Maize Breeding Station South, D–68307 Mannheim, Germany; [6] Corresponding author

With 7 tables

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Abstract

Sorghum, *Sorghum bicolor* L. Moench, is grown mostly in semi-arid climates where unpredictable drought stress constitutes a major production constraint. To investigate hybrid performance at different levels of drought stress, 12 single-cross hybrids of grain sorghum and their 24 parent lines were grown in eight site–season combinations in a semi-arid area of Kenya. In addition, a subset of 20 genotypes was evaluated at the seedling stage under polyethylene glycol (PEG)-induced drought stress. Environmental means for grain yield ranged from 47 to 584 g/m^2 reflecting the following situations: two non-stress, one moderate preflowering, four moderate terminal and one extreme drought stress. Mean hybrid superiority over mid-parent values was 54% for grain yield and 35% for above-ground biomass. Across environments, hybrids out-yielded two local varieties by 12%. Differences in yield potential contributed to grain yield differences in all stress environments. Early anthesis was most important for specific adaptation to extreme drought. Field performance was not related to growth reduction and osmotic adjustment under PEG-induced drought stress. In conclusion, exploitation of hybrid vigour could improve the productivity of sorghum in semi-arid areas.

Key words: *Sorghum bicolor* — drought escape — heterosis — osmotic adjustment — semi-arid areas — yield potential

Sorghum (*Sorghum bicolor* L. Moench) belongs to the major crops of the semi-arid tropics of Africa and Asia. One characteristic of semi-arid areas is the high variation in the amount of rain per season and in the rainfall distribution. Terminal drought stress prevails, however, dry spells can occur at any time during the growing season, leading to an unpredictable drought stress pattern. Further abiotic or biotic stress factors can be limiting in some areas or seasons. Local farmers are usually completely reliant on the drought resistance and yield stability of their rain-fed crop varieties.

Limited knowledge is available on the effects of hybrid vigour of sorghum under drought stress. Literature reports on the average mid-parent heterosis for grain yield in sorghum range from 13 to 127% with a mean of 46%. Lower values were usually obtained with crosses of adapted parent lines (Kambal and Webster 1966, Kirby and Atkins 1968, Reich and Atkins 1970, Liang et al. 1972), while high estimates were most often reported from studies that involved exotic germplasm (Niehaus and Pickett 1966, Laosuwan and Atkins 1977) and/or semi-arid growing conditions (Jowett 1972, Kapran et al. 1997).

Adaptation to drought stress may include drought escape, dehydration avoidance, and dehydration tolerance (Blum 1988). According to Ludlow and Muchow (1990), ‘matching phenology to water supply’ should receive highest priority when breeding sorghum for dry areas. In unpredictable environments, however, adjusting the number of days to anthesis and maturity is a difficult task. Early anthesis and/or a short duration of growth are advantageous in environments with terminal drought stress and where root growth is inhibited by physical or chemical barriers in the soil (Bidinger et al. 1987, Blum 1988, Blum et al. 1989). Later anthesis can be beneficial in escaping early season drought if the latter is followed by non-stress conditions (Bidinger et al. 1987, Blum 1988, Ludlow and Muchow 1990). In variable environments, therefore, long-term analyses of rainfall distributions may be undertaken (Ludlow and Muchow 1990) and the optimum dates of anthesis and maturity with respect to yield stability determined.

Osmotic adjustment has been proposed as a drought tolerance mechanism for several crop species (Shackel et al. 1982, Morgan 1984, Blum and Sullivan 1986, Morgan et al. 1986, Blum 1988, Ludlow and Muchow 1990). Sugar and potassium were identified as the main solutes contributing to the osmotic potential in sorghum (Premachandra et al. 1992). Osmotic adjustment was reported to minimize grain yield losses under controlled preflowering and postflowering drought in sorghum (Ludlow et al. 1990, Santamaria et al. 1990). Furthermore, sorghum and millet (*Pennisetum americanum* L. Leeke) landraces collected from drier regions displayed a greater osmotic adjustment compared with those from wetter places (Blum and Sullivan 1986). In the last study, the greater capacity for osmotic adjustment was associated with smaller plants, high rates of transpiration and low rates of leaf senescence under stress. No relationship between osmotic adjustment and grain yield under drought stress was found by Flower et al. (1990) and Tangpremsri et al. (1991a,b) for sorghum and by Guei and Wassom (1993) for maize (*Zea mays* L.). Similarly, populations of meadow fescue (*Festuca pratensis* Huds.) ranked differently when evaluated for drought resistance in pots from which water was withheld, and in the laboratory under artificial osmotic stress (Thomas et al. 1996). Girma and Krieg (1992a,b) showed that osmotic adjustment does not prevent reduction in stomatal

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Table 1: Designations and pedigrees of the hybrids used in the study

Set 1		Set 2	
Hybrid	Pedigree	Hybrid	Pedigree
SDSH 409[1]	Ma 6[1] × R 8602[1]	SDSH 300	ICSA 20 × SDS 170
SDSH 19[1]	ATX 623[1] × SDS 3219[1]	SDSH 48[1]	ICSA 12[1] × SDS 6013[1]
ICSH 110	ICSA 296 × ICSR 33	SDSH 339	ATX 631 × A 6352
SDSH 315	ICSA 21 × R 8609	SDSH 4[1]	D2 A[1] × SDS 3880[1]
SDSH 215[1]	SPL 23A[1] × MR 855[1]	SDSH 343[1]	A 150[1] × SDS 2690[1]
ICSH 205	ICSA 51 × ICSR 152	SDSH 398	A 8607[1] × ZAM 1518[1]

[1] Tested for growth rate and osmotic adjustment under PEG-induced drought stress.

Table 2: Site–season combinations, respective amount of water received (rain plus supplemental irrigation in some environments), environmental means for grain yield, type of drought stress and environmental codes allocated

Season[1] and year	Site[2]	Amount of water[3] (l/m^2)	Mean grain yield (g/m^2)	Type of drought stress	Code
SR 1991/92	Kibwezi A	430	584	Non-stress	N1
	Kibwezi B	373	297	Moderate terminal	D1
LR 1992	Kibwezi A	259	47	Extreme (preflowering and terminal)	D6
	Kibwezi C	275	154	Moderate terminal	D5
SR 1992/93	Kibwezi A	1078	537	Non-stress	N2
	Kiboko	597	284	Preflowering, followed by rains	D2
LR 1993	Kibwezi A	R + 173	222	Moderate terminal	D3
	Kiboko	R + 151	221	Moderate terminal	D4

[1] Two rainy seasons per year in Kenya: Short Rains (SR) and Long Rains (LR).
[2] A = Irrigation project, B = Goat Research Station, both University of Nairobi; C = local farm.
[3] R = Residual moisture from previous Short Rains.

conductance and photosynthesis in sorghum as water stress increases. Blum (1996) outlined that osmotic adjustment may not be a very effective mechanism of drought resistance under conditions where the development of drought is, by nature, very rapid.

In this contribution we present data on the performance of sorghum hybrids and lines, as well as the heterosis realized at different levels of drought stress in Kenya. Relationships between grain yield under stress, yield potential, date of anthesis and osmotic adjustment under polyethylene glycol (PEG)-induced drought stress are of additional interest. Data are taken from a more comprehensive study investigating the effects of heterozygosity and heterogeneity on the adaptation of sorghum to a semi-arid area of Kenya (Haussmann 1995).

Materials and Methods

The 12 unrelated single-cross hybrids of sorghum tested and their 24 parent lines represented a random sample of breeding materials from SADC/ICRISAT (Southern African Development Community/ International Crops Research Institute for the Semi-Arid Tropics) in Zimbabwe and ICRISAT-India. These materials were randomly divided into two sets (Table 1). Within both sets, lines (maintainer versions of cytoplasmic-genic male-sterile lines) and hybrids were each grown in homogeneous pure stands and in heterogeneous two-component mixtures. Each set was planted together with six control varieties, including the two local cultivars 'Makueni' and 'Seredo', in a 6 × 6 triple lattice design.

The experiment was conducted in eight macro-environments (site–season combinations) in the semi-arid Makueni District, Kenya, during 1991–93 (Table 2). The two lattices of Sets 1 and 2 were grown side by side in the same fields. Plots consisted of three or four rows, 3 or 4 m long with 0.8 m inter-row spacing, resulting in plot sizes between 9.6 and 12.8 m^2. All trials were hill-planted by hand with 0.2 m between hills, and thinned to one plant per hill. The total amount of water (rain plus irrigation) received by the individual experiments ranged from 151 to 1078 l/m^2. Supplemental irrigation for establishment of stands was given in some environments. Owing to lack of rain, experiments in the Long Rains 1993 relied on irrigation and residual soil moisture from the previous, outstandingly wet, Short Rains 1992–93. Soil types were chromic luvisol and luvisol at Kibwezi and Kiboko, respectively. Fertilizers were applied at Kibwezi A in the Short Rains 1991–92 (100 kg N/ha, 50 kg P_2O_4/ha, 50 kg K_2O/ha before planting) and at Kiboko in the Long Rains 1993 (50 kg N/ha, top-dressed). Chemical plant protection against insects was carried out when necessary. Birds were scared-off from flowering time onwards. Weeding was done by hand.

In addition to the field trials, a subset of 20 genotypes (Table 1) was evaluated in the laboratory under PEG-induced drought stress. Seeds were germinated in paper towels. Intact seedlings were transferred to continuously aerated nutrient solution in the growth chamber at 25/35°C night/day temperatures, with a 12 h photoperiod and 60 ± 7% relative humidity. After 14 days, half of the plants were moved to nutrient solution containing PEG 6000. Solution potentials of stress and control (pure nutrient solution) treatment were -0.71 MPa and > -0.01 MPa, respectively. A split plot design was used with stress regimes as main plots and genotypes as subplots. At 17 and 24 days after emergence six uniform plants (replicates) of each genotype were individually harvested in each treatment. Plants were weighed after drying at 85°C for 48 h and growth rates were calculated from the increase in dry weight over the seven days. Percentage of injury by PEG was derived from the growth rates under the two treatments. To obtain osmotic adjustment data, plants were moved at 24 days after emergence from PEG to pure nutrient culture for a recovery period of 24 h. Leaf samples were then taken and frozen at -18°C. Samples were later thawed and put in a Peltier thermocouple psychrometer (Decagon Inc., Pullman, WA, USA) to measure osmotic potentials. Osmotic adjustment was estimated from the difference in osmotic potential between PEG grown plants and control plants.

The computer programs PLABSTAT (Utz 1993) and PLABCOV (Utz 1994) were used for statistical analyses. Hybrid superiority was calculated relative to mid-parent, female, male and better-parent per-

Table 3: Means of lines and hybrids across eight environments (8E) and mean relative hybrid superiority across these and in the individual environments (N1, N2, D1–D6) for various traits, averaged over two sets of material

	Means (8E)		Hybrid superiority over lines (%) across all eight and in individual environments[2]								
Trait[1]	Lines	Hybrids	8E (293)	N1 (584)	N2 (537)	D1 (297)	D2 (284)	D3 (222)	D4 (221)	D5 (154)	D6 (47)
GY (g/m^2)	238.7	367.3	53.9**	53.0**	55.2**	50.3**	35.9**	60.8**	46.4**	87.9**	106.6**
BM (g/m^2)	717.5	968.8	35.0**	37.4*	36.3**	25.8**	24.5**	40.9**	34.2**	63.8**	27.2+
HI (%)	33.2	36.6	10.2**	4.3	12.1*	6.7+	6.0	3.4*	6.6	9.9	76.5*
NP ($/m^2$)	5.5	5.8	6.4*	1.9	1.0	5.5	−2.9	17.4*	9.5**	24.5**	1.9
H/P	1.1	1.2	6.1+	12.6*	5.9	1.0	0.0	−2.7	7.1+	11.4*	37.1**
K/H (× 100)	16.3	19.5	19.3**	6.2	23.8**	13.7	19.8	38.9*	17.1+	28.7+	31.4*
TG (g)	22.0	24.8	12.7**	25.6*	17.2**	16.7*	16.8**	1.3	6.6+	5.3	12.5
PH (cm)	121.2	167.4	38.2**	46.5**	43.0**	48.2**	34.6**	30.1**	29.8**	36.8**	28.7**
DA (d)	67.2	63.9	−4.9**	−6.1**	−3.7**	−4.4**	−5.4**	−5.0**	−7.5**	−3.4*	−3.2*
LG (%)	12.4	22.0	77.4*	–	–	–	–	97.0+	49.9*	291.7**	45.7+

+, *, ** Significant at P = 0.1, 0.05, and 0.01, respectively.

[1] GY = grain yield; BM = biomass; HI = harvest index; NP = plants/m^2, counted after 50% anthesis; H/P = heads per plant; K/H = kernels per head; TG = 1000-grain weight; PH = plant height; DA = days to anthesis; LG = percentage of lodging plants.

[2] N = non-stressed, D = drought stressed; for environmental codes see Table 2; environmental mean for grain yield (g/m^2) in brackets.

–, not assessed.

formance using lattice-adjusted entry means. Because genetic and environmental effects were related in a multiplicative manner, data were transformed logarithmically for combined analyses of variance across environments ($y = \ln(x + 1)$). Multiple regressions of grain yields in the stress environments on yield potential (average yield in two non-stress environments) and days to 50% anthesis were computed as suggested by Bidinger et al. (1987). The relative importance of grain yield potential and date of anthesis for grain yield under stress conditions was evaluated using standardized regression coefficients (Snedecor and Cochran 1980).

Results

Environmental means

Non-stress, preflowering, terminal, or extreme drought-stress conditions in the individual environments resulted in an extremely wide range of environmental means for grain yield (Table 2). In the following text the two non-stress environments will be named N1 and N2, and the six stress environments D1 to D6, respectively. The D-codes relate to decreasing yield levels. Low soil fertility, heavy rains followed by water logging and soil crustiness, and moderate pest or disease attack appeared as additional stress factors in single environments.

Relative hybrid superiority

The mean relative hybrid superiority over mid-parent values was greatest for grain yield, followed by plant height, and biomass (Table 3). The average hybrid superiority for grain yield components was lower than for grain yield. The highest values were found for number of seeds per head and 1000-grain weight. Hybrids, on average, flowered earlier and had a higher harvest index and many more lodging plants than the lines.

In the individual environments, the greatest relative hybrid superiority for grain yield was observed in the two lowest-yielding environments (D5, D6), indicating that grain yield under severe stress was reduced relatively less in hybrids than in lines (Table 3). For harvest index, the greatest hybrid superiority was obtained under extreme stress conditions (D6). For biomass, the relative hybrid superiority was highest in D5, but dropped to comparatively lower values in D6. The difference between hybrids and lines was only partly significant for yield components. Hybrid superiority was highest for number of seeds per head or 1000-grain weight in the majority of environments. Under extreme stress conditions (D6), a larger number of heads per plant was also an important component of the heterosis for grain yield. Hybrid superiority for the number of established plants was second among yield components in D3, D4 and D5. Two of these environments (D3, D5) were characterized by low mean plant densities (4.8 plants/m^2) and, therefore, by unfavourable conditions for plant establishment. The relative hybrid superiority for plant height was less under drought stress compared with non-stress conditions. No relationship between hybrid superiority and stress intensity became apparent for days to 50% anthesis and percentage of lodging plants.

The relative mid-parent heterosis for grain yield was larger under extreme drought stress than under non-stress conditions for eight hybrids, similar for two, and smaller for the remaining two hybrids (Table 4). Under non-stress conditions, the performance of the female parents was generally much poorer than that of the male parents, whereas under extreme drought stress the opposite was true with four hybrids of Set 1. The average relative hybrid superiority over the better parent was 32% and 59% under non-stress and stress conditions, respectively.

Comparison of hybrids with local varieties

Hybrids were, on average, superior to the local varieties 'Seredo' and 'Makueni' for grain yield, harvest index, number of seeds per head and 1000-grain weight, but did not differ significantly from them in biomass (Table 5). The grain yield performance of the best hybrid relative to 'Seredo' and 'Makueni' amounted to 126% and 116%, respectively, in Set 1 (hybrid SDSH 215), and 127% and 128%, respectively, in Set 2 (hybrid SDSH 398), across the eight environments. Both local varieties had more heads per plant, and 'Makueni' was significantly taller and flowered later than the average of the hybrids. The mean relative hybrid superiority over 'Seredo' decreased with increasing drought stress for grain yield. The reverse was true for the mean relative hybrid superiority over 'Makueni'.

Importance of yield potential and days to anthesis for grain yield under stress

A multiple regression of grain yields under stress on yield potential and days to 50% anthesis was computed for each stress

Table 4: Mean grain yield of the 12 hybrids, relative mid-parent heterosis (%), and relative hybrid superiority (%) over female and male parent in the two highest (N1, N2) and lowest (D5, D6) yielding environments, respectively

		Mean grain yield (g/m^2)		Rel. mid-parent heterosis (%)[1]		Rel. hybrid superiority (%)[1] over Female parent		Rel. hybrid superiority (%)[1] over Male parent	
Set	Hybrid	N1, N2	D5, D6	N1, N2	D5, D6	N1, N2	D5, D6	N1, N2	D5, D6
1	SDSH-409	642	146	49.1	50.3	132.2	38.5	9.8	64.1
	SDSH-19	713	149	44.7	48.6	67.3	69.4	27.5	32.3
	ICSH-110	715	113	67.9	163.1	123.6	194.0	34.5	137.6
	SDSH-315	672	129	54.0	73.2	61.7	64.1	47.0	81.7
	SDSH-215	782	175	60.3	137.0	105.5	117.8	31.3	160.3
	ICSH-205	628	109	61.4	61.2	74.1	33.0	50.4	96.8
	Mean	692	137	56.2	88.9	94.1	86.3	33.4	95.5
2	SDSH-300	668	148	39.8	72.2	89.6	152.7	10.8	30.7
	SDSH-48	696	136	40.4	131.9	67.4	187.1	21.0	94.4
	SDSH-339	690	80	63.4	30.9	63.6	35.4	63.3	26.8
	SDSH-343	685	118	50.4	90.8	123.1	153.7	13.4	53.1
	SDSH-4	778	124	57.9	35.9	171.0	46.9	11.5	26.2
	SDSH-398	767	215	80.7	106.6	98.0	216.3	66.1	53.3
	Mean	714	137	55.5	78.0	102.1	132.0	31.0	47.4

[1] Estimated from mean grain yields of the individual hybrids and parent lines in N1 and N2, and D5 and D6, respectively.

Table 5: Means of the local varieties 'Seredo' and 'Makueni', and mean relative performance of the hybrids compared to 'Seredo' and 'Makueni' across eight environments (8E), in two non-stress (N1, N2), and two extreme stress environments (D5, D6) for various traits, averaged over the two sets of material

	Local variety means (8E)		Hybrid performance (%) relative to 'Seredo'			Hybrid performance (%) relative to 'Makueni'		
Trait[1]	'Seredo'	'Makueni'	8E	N1, N2	D5, D6	8E	N1, N2	D5, D6
GY (g/m^2)	322	334	114*	113	99	110	106	112$^+$
BM (g/m^2)	904	1018	107	109	93	95	89	99
HI (%)	34.2	31.2	107*	108	108	117*	131*	114$^+$
H/P	1.5	1.4	79*	73*	81$^+$	86*	76*	96*
K/H	15.0	16.6	130*	127	129	118*	131$^+$	118
TG (g)	23.2	21.8	106	123	89	114*	113	106
PH (cm)	145	232	115	114	105	72*	65**	73*
DA (d)	65	67	98	97	98	94*	93*	95

$^+$, *, ** Difference between hybrids and the local variety significant at $P = 0.1$, 0.05, and 0.01, respectively.

[1] GY = grain yield; BM = biomass; HI = harvest index; H/P = heads per plant; K/H = kernels per head; TG = 1000-grain weight; PH = plant height; DA = days to anthesis.

Table 6: Relative importance (standardized regression coefficients) of yield potential and days to 50% anthesis for grain yield in six stress environments, and coefficients of determination (R^2) between actual and predicted grain yields, pooled over two sets of material

		Standardized regression coefficient for		
Environment[1]	Type of drought stress	Yield potential[2]	Days to 50% anthesis	R^2 (%)
D1	Moderate terminal	0.70**	−0.25**	66.1
D2	Preflowering, followed by rain	0.81**	0.21*	59.7
D3	Moderate terminal	0.65**	−0.18*	52.1
D4	Moderate terminal	0.71**	−0.09	55.3
D5	Moderate terminal	0.68**	−0.30**	67.9
D6	Extreme (preflowering and terminal)	0.22*	−0.60**	48.0

*, ** Significant at $P = 0.05$ and 0.01, respectively.

[1] For environmental codes see Table 2.

[2] Estimated from the average performance in the two non-stress environments, N1 and N2.

environment. Coefficients of determination ranged from 48 to 68% (Table 6). Under moderate stress intensities, standardized regression coefficients were comparatively higher for yield potential than for days to 50% anthesis. Under extreme drought (D6), the regression coefficient was much larger for days to 50% anthesis than for yield potential. A slight advantage of early anthesis was indicated for environments with moderate terminal drought (D1 and D3–D5), while in D2, characterized by preflowering stress followed by rains, a late onset of anthesis was slightly beneficial as, indicated by the positive standard

Table 7: Mean performance of parent lines and hybrids, and means and ranges of the relative heterosis for growth rates in control and PEG, the percentage of injury by PEG, and osmotic adjustment

	Means		Relative heterosis (%)	
Trait	Parents	Hybrids	Mean	Range
Growth rate in control (mg/day per plant)	9.8	14.6	51.5**	18–96
Growth rate in PEG (mg/day per plant)	4.0	4.1	7.5	−34–59
Injury by PEG (%)	56.4	71.3	26.4+	−32–51
Osmotic adjustment (MPa)	0.83	0.57	−28.7+	−51–−2

+, ** Significant at P = 0.1 and 0.01, respectively.

regression coefficient for days to 50% anthesis in this environment.

Growth rate and osmotic adjustment under PEG-induced drought stress

For growth rates under PEG stress vs. control nutrient solution, variation resulting from treatments, genotypes, and genotype × treatment interaction was highly significant (data not presented). No relationship existed between growth rates in PEG and the control, reflecting the differential reaction of the genotypes to the stress treatment. Wide ranges among entries were obtained for the percentage injury (42.5–82.4%) and for osmotic adjustment (0.25–1.09 MPa). The correlation between the percentage injury and osmotic adjustment was $r = -0.61$ (P = 0.01). Mean relative heterosis for growth rate decreased from control to the stress treatment (Table 7). The growth rate was therefore reduced relatively more by PEG in hybrids than in lines. An average negative heterosis of −29% was found for osmotic adjustment. Hybrids differed significantly (P = 0.01) in the heterosis estimates for percentage injury and osmotic adjustment.

Neither growth rate in PEG nor the percentage injury by PEG, nor the osmotic adjustment data were correlated with mean grain yield, yield potential or grain yield under severe stress conditions, biomass, or harvest index.

Discussion

Effects of hybrid vigour

In the present study, heterozygosity proved to be an important prerequisite for obtaining high grain yield of sorghum grown in semi-arid climates. The mean relative superiority of hybrids over mid-parent values for grain yield (54%) lies above the average estimate reported for sorghum in the literature. African hybrid breeding programmes with sorghum have used female parents descended from American lines in combination with African restorer genotypes (Doggett and Jowett 1966, Majisu and Doggett 1972). Lack of adaptation of the female lines can result in a lower mid-parent performance but may be overcome in hybrids by the 50% 'adapted' genome from the male parent, leading indirectly to above-average heterosis estimates. In fact, the female parents used in the present study generally had a lower mean grain yield than the restorer lines and were also inferior to the two local varieties. However, four of them proved to be specifically adapted to extreme stress conditions (among the highest-yielding genotypes in D6). The comparatively good performance of the two local varieties 'Makueni' and 'Seredo' could have resulted in part from a certain degree of heterozygosity and heterogeneity.

The relative hybrid performance varied with the environmental conditions. In the present study, estimates of the relative hybrid superiority for grain yield were greatest in the two lowest-yielding environments. However, this could not be confirmed in a second experiment carried out with sorghum in the Kibwezi/Kiboko region. In that experiment, three sets of factorial crosses between four female and four male SADC/ICRISAT inbred lines were each evaluated in eight site–season combinations with environmental means for grain yield between 167 and 596 g/m^2. Estimates of the relative hybrid superiority for grain yield ranged from 32 to 68%, with the highest estimate obtained under moderate stress conditions (Haussmann et al. 1998). An increasing relative superiority of sorghum hybrids over mid-parent values and varieties with increasing environmental stress was reported by Doggett and Jowett (1966) and Osmanzai (1994). Kapran et al. (1997) reported heterosis values of 45% under irrigation and 66% in rain-fed conditions. In the same tests, hybrids out-yielded local controls by 61% with irrigation and by 49% under rain-fed conditions. In contrast, Doggett (1969) and Kirby and Atkins (1968) described a rather stable average expression of heterosis for each of various characters across environments. Disparate results have also been obtained from other crop species. In primary hexaploid triticale (× *Triticosecale* Wittmack), the average relative heterosis was greater in an unfavourable than in a favourable year (Oettler et al. 1988). Sinolinding and Chowdhry (1974) found significant heterosis for wheat grain yield under irrigation (up to 17%) while little or negative heterosis occurred under moisture stress (−36 to 7%). In pearl millet, the yield advantage of topcross hybrids over landraces was 15–25% in an arid environment, and increased to 30–40% in the favourable environment. The greatest yield differences (40–80%) were observed in a terminal stress environment where the hybrids effectively escaped drought stress by flowering earlier (Bidinger et al. 1994). Obviously, the relationship between heterosis and environmental productivity depends on the materials included in the study, as well as on the type and intensity of environmental stresses and the importance of specific resistance or tolerance mechanisms. Better performance of hybrids under unfavourable 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.

Faster vegetative plant development is a most useful effect of hybrid vigour in many semi-arid sorghum-growing areas. The higher percentage of lodging plants in heterozygous entries is, in contrast, disadvantageous. It is therefore imperative to improve the genetic resistance of heterozygotes to lodging under terminal drought stress. The observed effects of heterozygosity for characters other than grain yield generally support previous findings in sorghum (Kambal and Webster 1966, Kirby and Atkins 1968, Liang et al. 1972).

Growth data under PEG-induced stress indicated lower osmotic adjustment and a higher percentage of injury by PEG in hybrids compared with lines, thereby confirming earlier observations made by Basnayake et al. (1994). These authors reported a difference between hybrids and lines of −0.29 MPa and suggested a tendency for high osmotic adjustment to be inherited in a recessive manner, as found for wheat (Morgan 1984). Conversely, the lower osmotic adjustment in hybrids may also be associated with their larger cell sizes and may therefore reflect a type of dilution effect.

Reconciliation of stress tolerance and yield potential

As to whether stress tolerance and yield potential can be combined in an individual genotype, results from the present study supported the conclusion made by Acevedo and Fereres (1993) and Sadiq et al. (1994) that, at least up to a certain degree of stress, varieties with a high yield potential (e.g. hybrids) may yield more than highly stress-tolerant varieties (e.g. some of the female parents). Only under severe stress may specific adaptation mechanisms (e.g., escape) become more important than yield potential (Bidinger et al. 1994).

Indirect selection traits

Indirect selection traits need to be easy, cheap, and quick to measure, so that high selection intensities can be realized in early generation testing. Furthermore, indirect traits must be highly heritable and closely correlated to the target trait, in our case grain yield in semi-arid environments. In the present study, early anthesis appeared to be the only character to meet the foregoing requirements. Selection for early anthesis may be expected to contribute to gains not only in grain yield performance but also in yielding stability (Blum et al. 1989, Ludlow and Muchow 1990).

According to Blum (1993), osmotic adjustment values greater than 0.3 MPa provide an advantage for plant growth under drought. The values of 0.83 and 0.57 MPa obtained in lines and hybrids, respectively, should therefore be effective. Since drought stress in the field generally developed slowly, i.e. within 1−2 weeks, there should have been enough time for the plants to activate their potential for osmotic adjustment. In contrast, variation for osmotic adjustment did not explain differences among lines or hybrids in stress tolerance under field conditions. These results, as well as those of Flower et al. (1990), Tangpremsri et al. (1991a,b), Guei and Wassom (1993), and Thomas et al. (1996) show that the corroboration of a positive effect of osmotic adjustment on yield under field conditions is difficult. This is not surprising, since the frequency, timing and intensity of stress varies among environments, and different combinations of yield components or morpho-physiological traits can give similar yields in a given stress situation (Ludlow and Muchow 1990, Ceccarelli et al. 1991, van Oosterom and Acevedo 1992, Acevedo and Fereres 1993). Studies with barley landraces in Syria indicated that natural and artificial selection have been unable to identify a particular trait associated with superior performance across environments or an ideotype with a specific architecture of different traits, but have led to an architecture of genotypes, each representing different combinations of traits (Ceccarelli 1994).

Consequences for sorghum improvement in semi-arid areas

The large amount of hybrid superiority observed in East and West African environments in the present and other studies make hybrid sorghum breeding a promising approach for semi-arid areas. However, while heterosis was found here to be well expressed in low-yielding (stress) environments, the fact remains that the absolute yield of the hybrids is still low in such environments so that the small-scale farmer may not be able to afford hybrid seed with the revenue. Hence, hybrids will remain an economical and viable option mainly for the farmers in the higher-yielding environments.

Instead of hybrids, synthetics could be produced to take advantage of heterosis. This type of variety can be regrown for a few seasons without serious changes in genetic composition. Because sorghum is a predominantly self-pollinated crop, it may be necessary to increase the outcrossing rate by incorporating male-sterility genes or by transferring incompatibility genes from other grass species by embryo culture techniques or genetic engineering.

Early anthesis was shown to be an important indirect selection trait for specific adaptation to terminal drought. Furthermore, results indicated that selection for grain yield under non-stress conditions may indirectly improve productivity under stress. However, the occurrence of different stress factors and variable stress intensities in semi-arid areas, and the importance of genotype × environment interaction, necessitate the evaluation of the breeding materials under a wide range of growing conditions. In defining selection criteria, emphasis should be put on specific adaptation to extreme drought stress, since achieving a certain minimum grain yield is more important for subsistence farmers than increased yields in the rare favourable seasons.

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