Quantitative-genetic parameters of sorghum [*Sorghum bicolor* (L.) Moench] grown in semi-arid areas of Kenya

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Summary

Low and erratic rainfall constitutes a major constraint to sorghum production, and impedes sorghum improvement in semi-arid tropics. To estimate quantitative-genetic parameters for sorghum under variable stress conditions, three sets of factorial crosses between four by four lines each were grown with parents and a local cultivar in eight macro-environments in semi-arid areas of Kenya. Fourteen traits were recorded including grain yield, above-ground drymatter, harvest index, days to anthesis, leaf rolling score, and stay-green. Environmental means for grain yield ranged from 167 to 595 g m^{-2}. Mean hybrid superiority over mid-parent values was 47, 31, and 9% for grain yield, above-ground drymatter, and harvest index, respectively. Differences among both lines and hybrids were highly significant for all traits. Genotype × environment interaction variances were larger than genotypic variances for grain yield, above-ground drymatter, and harvest index. Corresponding heritabilities ranged between 0.72 and 0.84. Variation among hybrids was determined by GCA and SCA effects for most characters. Predominance of additive-genetic effects was found for grain yield components, plant height, and leaf rolling score. Lack of variation in GCA was noted among female lines for major performance traits. While low leaf rolling score was correlated with high grain yield, there was no such association for stay-green. Hybrid breeding could contribute to sorghum improvement for semi-arid areas of Kenya. To increase selection progress for major performance traits, genetic variation among female lines should be enhanced. Importance of genotype × environment interaction underlines the necessity of evaluating breeding materials under a broad range of dryland conditions.

Abbreviations: GYP = grain yield; AGD = above-ground drymatter; HI = harvest index; P m^{-2} = plants m^{-2}; H/P = heads per plant; K/H = kernels per head; TGW = 1000-grain weight; DAN = days to 50% anthesis; PHT = plant height; DFL = days to first leaf rolling symptoms: D4L = days until the four lowest leaves were dry; LRS = leaf rolling score around flowering; NGL95 = number of green leaves at 95 days after planting; NLP = percentage of non-lodging plants; LP = percentage of lodging plants.

Introduction

Sorghum is an important component in traditional farming systems and in diets of millions of people in the semi-arid tropics. In Eastern Africa, more than 70% of sorghum are cultivated in the dry and hot lowlands (Mukuru, 1993). Low soil fertility, poor stand establishment, a highly unpredictable drought stress pattern and high micro-variability within fields are major production constraints which also complicate sorghum improvement in these areas.

Estimates of quantitative-genetic parameters are necessary for computing the expected gain from direct or indirect selection, for optimizing selection strategies like the allocation of resources to number of replications, test environments and seasons, or for

assessing the potential merit of a hybrid program in a crop species. However, most quantitative-genetic studies with sorghum were conducted in the United States of America or in India, and do not refer to extreme and variable drought stress, or include only two or three environments (Kambal & Webster, 1965; Niehaus & Pickett, 1966; Beil & Atkins, 1967; Collins & Pickett, 1972; Jan-Orn et al., 1976; Singhania, 1980; Bittinger et al., 1981; Finkner et al., 1981; Mishra et al., 1992). Estimates obtained in those studies are therefore not directly applicable to the situation in semi-arid areas. In contrast, the present experiment was conducted across eight site/season combinations, all of them under unpredictably variable dryland conditions. Our objectives were to estimate heterosis, components of the genetic variance, heritability coefficients, genotype × environment interaction variances, genetic correlations between traits and between line performance and general combining ability (GCA) effects for various traits of sorghum under semi-arid conditions in Kenya.

Materials and methods

Genetic materials consisted of three sets of factorial crosses between four female and male lines each (Table 1). The parent lines represented a random sample of actual breeding materials from SADC/ICRISAT (Southern African Development Community/ International Crops Research Institute for the Semi-Arid Tropics).

The 16 crosses of each set were planted together with their 8 parent lines (using the maintainer versions of the cytoplasmic-genic male sterile lines) and the improved Kenyan variety 'KAT-369' in 5 × 5 triple lattice designs. The three sets were grown side by side. The experiment was conducted in eight macro-environments (site/season combinations) in Kenya, during 1992 and 1993 (Table 2). Plots consisted of four rows, three or four meters long with 0.8 m inter-row spacing, resulting in plot sizes between 9.6 and 12.8 m^2. The nominal plant density was 6.25 plants m^{-2}. The total amount of water (rain plus supplementary irrigation) received by the individual experiments ranged from 150 to 1078 lm^{-2}. Supplementary irrigation for stand establishment was given in all environments except at Kibwezi C. Due to lack of rains, experiments had to be raised completely with irrigation in the Long Rains 1993. Residual soil moisture from the outstandingly wet Short Rains 1992–93 may

have supported plant growth in the Long Rains 1993. Likewise, residual moisture from previous, irrigated crops might have contributed to the growth of the trials inside the Kibwezi Irrigation Project (Kibwezi A-1). Soil types were Chromic Luvisol at Kibwezi, Eutric Fluvisol at Perkerra, and Luvisol at Kiboko. Topdressing with urea took place at a rate of 50 kg N ha^{-1} only at Kiboko in both Short Rains 1992/93 and Long Rains 1993. Plants were chemically protected against insects when necessary. Birds were scared from flowering time onwards. Weeding was done by hand.

The following traits were recorded or calculated on a plot basis: grain yield [GYP, g m^{-2}] at 9.5 to 10.5% grain moisture, estimated on the basis of the whole four-row plot and linearly corrected in the event of bird or squirrel damage; total above-ground drymatter [AGD, g m^{-2}]; harvest index [HI,%]; number of established plants m^{-2} after anthesis [P m^{-2}]; number of heads per plant [H/P]; number of kernels per head [K/H]; 1000-grain weight [TGW, g], based on a sample of 250 grains from the center rows; plant height from ground to the tip of the panicles [cm]; days to 50% anthesis [DAN, d]; days to first leaf rolling symptoms [DFL, d]; days until the four lowest leaves were dry [D4L, d] as measure of senescence; leaf rolling score around anthesis [LRS]; score: 1 = no leaf rolling, 9 = maximum leaf rolling of all leaves with the leaf colour changing to olive green; number of green leaves per plant (as measure of stay-green) counted at 95 days after planting and averaged over ten plants of the center rows [NGL95]; and percentage of lodging [LG,%] respective non-lodging plants [NLP,%] at harvest.

The computer programs PLABSTAT (Utz, 1993) and PLABCOV (Utz, 1994) were used for statistical analyses. Both genotypes and environments were considered as random factors. The crosses D 2A × SDS 1835, ICSA 19 × SDS 3194, and ICSA 19 × SDS 1835 (all in Set 1) were partially sterile in some environments. The corresponding data were discarded and replaced by missing values in further analyses. Repeatabilities were computed as the ratio between the treatments component of variance and the sum of the latter and the effective error variance (Utz, 1993). Hybrid superiority was expressed relative to mid-parent performance. Broad-sense heritabilities were estimated as described by Allard (1960). The importance of specific combining ability (SCA) effects was expressed as ratio of SCA to the total genotypic variance (sum of GCA variance of females, GCA variance of males, and SCA variance). Genetic correlations

Table 1. Parent lines[a] used in the three sets of factorial crosses

Set 1		Set 2		Set 3	
Females	Males	Females	Males	Females	Males
D2 A	SDS 238	SPL 10A	MR 809	SPL 23A	SDS 3219
ICSA 19	SDS 1835	SPL 109A	MR 830	A 145	SDS 4261
ICSA 12	SDS 3194	SPL 177A	MR 855	A 150	R 8602
ICSA 21	SDS 3880	ATX 623	SPL 28R	A 8617	R 8609

[a] D = Dwarf; ICSA = ICRISAT Sorghum A-line; SDS = SADC Sorghum; SPL = Sorghum Pure Line; ATX = A-line from Texas A&M University/Agricultural Experiment Station; MR = Male R-line; A = A-line; R = R-line.

Table 2. Site/season combinations, amount of water [$l\,m^{-2}$] received by the individual experiments, environmental means, repeatabilities (Rep.), and coefficients of error variation (CV) for grain yield in the eight environments, and definitions of type of drought stress observed in the individual environments

Season[a]	Site[b]	Amount of water[c] [$l\,m^{-2}$]	Grain yield			Type of drought stress
			Mean [$g\,m^{-2}$]	Rep. [%]	CV [%]	
LR 1992	Kibwezi A-1	R+281	563	94.2	9.7	Non-stress
	Perkerra	300+F	387	82.4	20.3	Preflowering + terminal
SR 1992–93	Kibwezi A-2	1078	595	97.0	8.5	Non-stress (N1)
	Kibwezi C	954	295	93.9	12.6	Terminal
	Kiboko	603	253	89.4	16.6	Terminal
LR 1993	Kibwezi A-1	R+150	300	80.2	22.3	Terminal
	Kibwezi A-2	R+173	271	90.7	13.4	Terminal
	Kiboko	R+186	167	87.7	18.7	Terminal

[a] LR = Long Rains; SR = Short Rains.
[b] A = Irrigation Project; –1: previous crop fully irrigated; –2: previous crop rainfed or fallow; C = Local Farm.
[c] R = Residual moisture from previous rainy season or irrigated crop. F = Furrow irrigation.

were computed following Method 1 of Henderson (Searle, 1971).

Results

Means and accuracy of the individual experiments

Growing conditions during the experimental period comprised two non-stress and six stress environments (including moderate to severe preflowering and/or terminal drought), with corresponding environmental means for grain yield ranging from 595 to 167 g m^{-2} (Table 2). In the lowest yielding environment (Kiboko in the Long Rains 1993), grain yield and above-ground drymatter were reduced to a similar extent, i.e., to 28 and 31% of the performance in the non-stress environment N1, respectively. The accuracy of the data in the individual environments as reflected in the coeffi-

cient of error variation ranged between 8.5 and 22.3% for grain yield, and was similar or lower for most of the other traits. Repeatabilities for grain yield ranged between 80% and 97%. The estimates were highest under non-stress conditions, and lowest at Perkerra in the Long Rains 1992, and at Kibwezi A-1 in the Long Rains 1993. The growing conditions at Perkerra were characterized by very variable drought stress intensities across the field due to uneven furrow irrigation. Severe preflowering drought stress symptoms were observed in some parts of the field in this environment.

Hybrid superiority

Combined across the eight environments and the three sets of material, the mean relative hybrid superiority over the mid-parent values was highest for grain yield, followed by plant height and above-ground drymatter (Table 3). Hybrid vigour was expressed in a higher

Table 3. Means of lines and hybrids, and mean relative hybrid superiority for 14 traits, averaged over three sets of material and the indicated number of environments

Trait[a]	N. of environ.	Means		Rel. hybrid superiority [%]
		Lines	Hybrids	
GYP [g m^{-2}]	8	274	403	47.1**
AGD [g m^{-2}]	8	767	1001	30.5**
HI [%]	8	36.0	39.1	8.6**
P m^{-2}	8	5.8	6.1	5.2**
H/P	8	1.25	1.31	4.8**
K/H [× 100]	8	15.5	18.0	16.1**
TGW [g]	8	24.3	27.5	13.2**
DAN	8	68	65	−4.4**
PHT [cm]	8	123	166	35.0**
DFL [d]	8	53	55	3.8+
D4L [d]	5[b]	90	89	−1.1+
LRS [units]	8	4.3	3.8	−11.6**
NGL95	7[c]	4.4	4.2	−4.6*
NLP [%]	5[b]	99	80	−19.2+

+, *, ** Difference between lines and hybrids significant at the 0.1, 0.05, and 0.01 probability levels, respectively.
[a] For trait abbreviations see list of abbreviations.
[b] One non-stress and four stress environments.
[c] One non-stress and six stress environments.

harvest index, earlier anthesis, later beginning of leaf rolling symptoms, and lower leaf rolling scores around anthesis, less green leaves at 95 days after planting, and more lodging plants. Heterosis for the number of kernels per head and 1000-grain weight contributed most to heterosis for grain yield.

The relative hybrid superiority varied significantly across environments for all traits except the percentage of lodging plants. Hybrids significantly outyielded the lines for grain yield, above-ground drymatter, and harvest index under all conditions. There was no relationship between amount of hybrid superiority and intensity of stress as measured by the environmental mean for grain yield.

The average relative hybrid superiority over the local improved cultivar 'KAT-369' was 14% for grain yield, and 19% for above-ground drymatter. 'KAT-369', on the other hand, had a 2.4% higher harvest index, averaged over the eight environments.

The frequency distribution of the entries for grain yield, averaged across the eight environments shows lines and hybrids as two overlapping groups (Figure 1). The local check 'KAT 369' lied between the two groups. Within the lines, most female lines were lower yielding than the male lines.

Variance components and heritabilities

Across environments, genetic variances among lines and among hybrids were highly significant for all traits (Table 4). With the lines, genotype × environment interaction variances were larger than the genetic variances for grain yield (1.7 fold), above-ground drymatter (1.9 fold), harvest index (2.0 fold), number of established plants m^{-2} (3.2 fold), days until the four lowest leaves were dry (1.5), and the number of green leaves at 95 days after planting (2.7 fold). The respective estimates of broad-sense heritabilities were moderate to high, ranging between 0.63 and 0.79. High heritability estimates were obtained for most other traits. With the hybrids, genotype × environment interaction variances were larger than the genetic variances for grain yield (1.1 fold), above-ground drymatter (1.9 fold), harvest index (1.1 fold), and days to first leaf rolling symptoms (1.5 fold). Estimated heritabilities were generally in the same order of magnitude as those obtained for the lines.

Variation of GCA effects was important for all traits studied (Table 5). While the GCA variance was highly significant among males for major performance traits, it was non-significant among females for grain yield, above-ground drymatter, harvest index, and
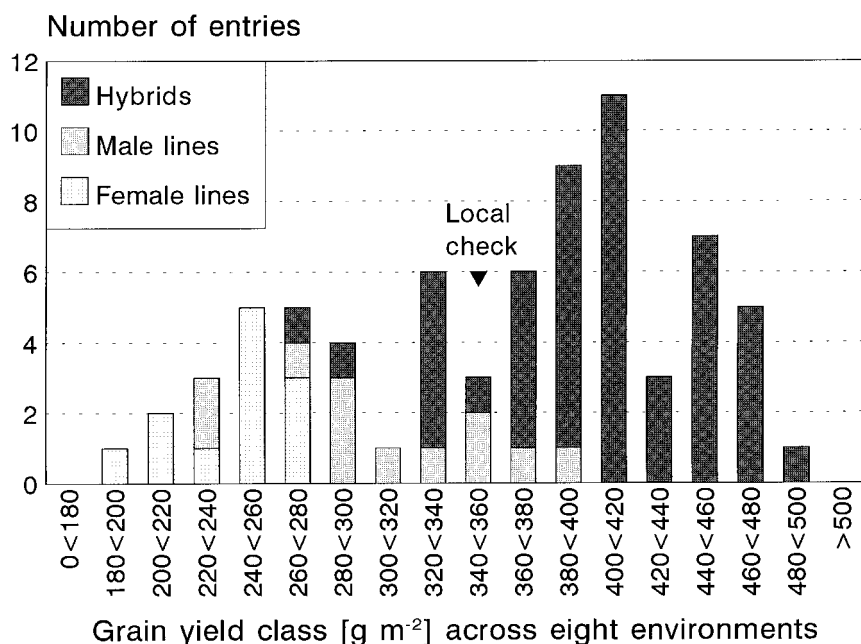
Number of entries

Figure 1. Frequency distribution of 12 female lines, 12 male lines, and 48 F_1 hybrids of sorghum, and performance class of the local check 'KAT 369' for mean grain yield, averaged across eight environments in semi-arid areas of Kenya.

Table 4. Estimated variance components and broad-sense heritabilities (h^2) of lines and hybrids for 14 traits, pooled over three sets of material and combined across the indicated number of environments

Trait[a]	N. of environ.	Source of variation					h^2	
		Lines	Hybrids	Line × environ.	Hybrid × environ.	Error	Lines	Hybrids
GYP	8	17.4**	21.0**	29.1**	23.7**	27.1	0.79	0.84
AGD	8	64.6**	46.2**	123.2**	85.9**	140.4	0.75	0.74
HI	8	6.2**	5.9**	12.0**	6.2**	22.0	0.72	0.78
P m^{-2}	8	2.5**	0.1*	8.0**	neg.	12.1	0.63	0.92
H/P[b]	8	1.5**	1.1**	0.4*	0.1	2.9	0.90	0.89
K/H[b]	8	6.8**	7.4**	1.1	2.8**	21.8	0.87	0.86
TGW	8	12.1**	4.6**	2.7**	2.0**	5.3	0.96	0.91
DAN	8	5.2**	1.7**	2.2**	0.9**	3.1	0.93	0.88
PHT	8	207.2**	623.2**	30.7**	102.5**	116.4	0.97	0.97
DFL	8	43.0**	12.0**	37.3**	18.4**	13.8	0.89	0.81
D4L	5[d]	5.4**	5.6**	8.3**	4.7**	19.2	0.65	0.80
LRS[c]	8	9.5**	2.3**	1.7**	1.0**	3.1	0.97	0.90
NGL95[c]	7[d]	1.4**	1.4**	3.8**	1.2**	5.9	0.63	0.78
LG	5[d]	20.4**	75.5**	0.8	24.1*	238.1	0.56	0.85

*, ** F-test significant at the 0.05 and 0.01 probability levels, respectively; neg. = negative estimate.
[a] For trait abbreviations see list of abbreviations.
[b,c] Estimates of variance multiplied by 100 and 10, respectively.
[d] Environments as indicated in Table 3.

Table 5. Estimated components of variance due to GCA in females (f) and males (m), SCA, and corresponding interactions with the environments (E) for 13 traits, pooled over the three sets of material and combined across the indicated number of environments

Trait[a]	N. of environ.	Variance due to					
		GCA(f)	GCA(m)	SCA	GCA(f) × E	GCA(m) × E	SCA × E
GYP	8	neg.	32.5**	11.7**	7.7**	25.5**	6.4**
AGD	8	1.9	82.4**	15.9**	24.0**	111.3**	29.1**
HI[c]	8	0.7	54.9**	17.4**	2.7	52.9**	30.6*
H/P[b]	8	14.5**	23.3**	0.8	1.7**	1.6**	neg.
K/H	8	0.9*	9.8**	1.0*	neg.	2.3**	2.5+
TGW[c]	8	4.5**	56.4**	2.2**	5.2**	31.8**	1.4
DAN[c]	8	11.6**	3.0+	8.1**	4.2**	6.3**	1.2
PHT	8	47.3**	764.5**	14.3**	26.4**	122.0**	17.9**
DFL	8	5.3**	9.1**	0.4	4.7**	5.1**	13.4**
D4L	5[d]	0.8	4.9**	1.3**	1.4*	1.6*	3.1**
LRS[b]	8	5.7**	17.1**	3.2**	2.8**	4.4**	6.3**
NGL95[b]	7[d]	7.3**	2.1	6.8**	2.8*	18.3**	0.2
LG	5[d]	4.8	61.2**	10.8+	neg.	neg.	neg.

[+], [*], [**] F-test significant at the 0.1, 0.05 and 0.01 probability levels, respectively; neg. = negative estimate.
[a] For trait abbreviations see list of abbreviations.
[b,c] Estimates of variance multiplied by 100 and 10, respectively.
[d] Environments as indicated in Table 3.

Table 6. Estimated coefficients of genetic correlation (r_G) between the performance of lines *per se* and their GCA for 12 traits, combined across three sets of material and the indicated number of environments

Trait[a]	N. of environ.	r_G	
		Females	Males
GYP	8	–[c]	0.93++
AGD	8	*0.56*[+d]	1.07++
HI	8	*0.39*[d]	0.16
H/P	8	0.84++	0.98++
K/H	8	0.62++	0.77++
TGW	8	0.45+	0.54++
DAN	8	0.43+	0.52+
PHT	8	0.85++	0.94++
DFL	8	0.58++	0.99++
D4L	8	*0.88*[++d]	0.52
LRS	8	0.82++	0.89++
NGL95	7[b]	0.75++	*0.81*[++d]

[+], [++] Estimate exceeds its standard error once or twice, respectively.
[a] For trait abbreviations see list of abbreviations.
[b] Environments as indicated in Table 3.
[c] Not computed due to negative estimate of the GCA variance component.
[d] Coefficients printed in italics refer to traits for which no significant GCA variance was found.

days until the four lowest leaves were dry. On the other hand, the GCA variance among males was relatively small or non-significant for days to anthesis and the number of green leaves at 95 days after planting.

The variance of SCA effects was also significant for all traits except number of heads per plant and days to first leaf rolling symptoms. The percentage ratio of SCA to the total genotypic variance was 42% for the number of green leaves at 95 days after planting, 27% for grain yield, 24% for harvest index, 19% for days until the four lowest leaves were dry, 16% for above-ground drymatter, 14% for the percentage of lodging plants, 12% for the leaf rolling score, and less than 10% for the number of kernels per head, 1000-grain weight, and plant height.

The interaction between GCA and environments was significant for all traits except the percentage of lodging plants and was, on average, equal or larger than the average variance of GCA for grain yield, above-ground drymatter, harvest index, and number of green leaves at 95 days after planting. Significant SCA × environment interaction occurred for grain yield, above-ground drymatter, harvest index, number of kernels per head, plant height, days to first leaf rolling symptoms, and leaf rolling score. The variance component estimates were generally larger than those for the SCA variance.

Relationship between line performance and GCA

Coefficients of genetic correlation between the performance of lines *per se* and their GCA differed largely between females and males for grain yield and above-ground drymatter (Table 6). There was no significant relationship for harvest index. Moderate to tight genetic correlations between line performance and GCA were obtained for number of heads per plant, kernels per head, plant height, days to first leaf rolling symptoms, and leaf rolling score. Moderate to low correlations were found for 1000-grain weight and days to anthesis.

Relationships among traits

In both lines and hybrids high grain yield was associated with high above-ground drymatter, tallness, delayed leaf rolling, low leaf rolling score around anthesis, early drying up of the four lowest leaves, and a higher percentage of lodging plants (Table 7). A weak positive correlation was obtained between grain yield and days to anthesis for lines when all eight environments were included in the calculations. The correlation turned to be non-significant when the analysis was done across the six stress (lowest yielding) environments only. A lower number of green leaves at 95 days after planting was weakly associated with higher grain yield among the hybrids. High above-ground drymatter was associated with late anthesis, delayed leaf rolling, low leaf rolling score, and early drying up of the four lowest leaves. High harvest index was accompanied by early anthesis, delayed leaf rolling, lower leaf rolling score, and lower number of green leaves at 95 days after planting. Compensation among grain yield components was reflected by the negative correlation between the number of heads per plant and kernels per head, and between the number of kernels per head and 1000-grain weight. The genetic correlations were generally more tight for lines than for hybrids.

Discussion

One characteristic of semi-arid areas is the large variability of environmental conditions across seasons and across locations. This was reflected in the large range of environmental means for grain yield obtained in the present as well as in other studies conducted in East African dryland areas (Jowett, 1972).

The superiority of hybrids over mid-parent values observed in the present study clearly points to the potential merit of a sorghum hybrid breeding program for semi-arid areas in Kenya. The obtained mean relative hybrid superiority of 47% was substantial and lies within the range, though at the upper limit, given for sorghum in the literature. African hybrid breeding programs in sorghum have been using female parents descendant from American lines in combination with African restorer genotypes (Majisu & Doggett, 1972). Low grain yield due to lack of adaptedness 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, most of the female parents used in the present study had a lower mean grain yield than the restorer lines and were inferior to the local variety as well. Similar results were obtained in a second experiment conducted in the same region with 12 unrelated hybrids and their 24 parent lines (Haussmann et al., 1998).

There was significant genetic variance among both lines and crosses for all traits considered. Lack of variation in GCA was observed among the tested female lines for major performance traits. Therefore, the genetic variation in the gene pool of cytoplasmic-genic male sterile lines should be enhanced, in order to increase selection progress in hybrid breeding for grain yield, above-ground drymatter, and harvest index. An integration of locally adapted germplasm into breeding programs for extreme and variable stress environments was advocated by Weltzien & Fischbeck (1990), Ceccarelli & Grando (1991), and Ceccarelli (1994). Topcrossing of landraces on improved female parents has been recommended for pearl millet [*Pennisetum americanum* (L.) Leeke] by Mahalakshmi et al. (1992) and Bidinger et al. (1994). With this method, the genetic heterogeneity, yielding stability and stress tolerance of the landraces was combined with the higher yield potential of the seed parent lines. Furthermore, the great genetic distance between landraces and improved lines should lead to high heterosis in such topcross hybrids.

Tight correlations between performance of the lines *per se* and their GCA confirmed the preponderance of additive genetic effects for most morphological and developmental traits. Similar results were reported by Kambal & Webster (1966), Niehaus & Pickett (1966), Beil & Atkins (1967), Laosuvan & Atkins (1977), and Hookstra et al. (1983). The significant contribution of SCA effects to hybrid perfor-

Table 7. Coefficients of important genotypic correlations among traits in the lines and in the hybrids, estimated across three sets of material and the indicated number of environments

Type of relationship	Correlated Traits[a]		N. of environ.	Genotypic correlation coeff.	
				Lines	Hybrids
Positive	GYP	× AGD	8	0.97^{++}	0.83^{++}
	GYP	× DAN	8	0.43^{++}	0.13
	GYP	× PHT	8	0.89^{++}	0.80^{++}
	GYP	× DFL	8	0.95^{++}	0.58^{++}
	GYP	× LG	5^{b}	0.95^{++}	0.44^{++}
	AGD	× DAN	8	0.68^{++}	0.41^{++}
	AGD	× DFL	8	0.86^{++}	0.44^{++}
	HI	× DFL	8	0.64^{++}	0.32^{+}
Negative	GYP	× LRS	8	-0.80^{++}	-0.59^{++}
	GYP	× D4L	5^{b}	-0.88^{++}	-0.84^{++}
	GYP	× NGL95	7^{b}	0.13	-0.47^{++}
	AGD	× LRS	8	-0.72^{++}	-0.50^{++}
	AGD	× D4L	5^{b}	-0.93^{++}	-0.71^{++}
	HI	× DAN	8	-0.43^{+}	-0.66^{++}
	HI	× LRS	8	-0.52^{++}	-0.16
	HI	× NGL95	7^{b}	-0.63^{+}	-1.16^{++}
	H/P	× K/H	8	-0.59^{++}	-0.26^{+}
	K/H	× TGW	8	-0.50^{++}	-0.63^{++}

[a] For trait abbreviations see list of abbreviations.
[b] Environments as indicated in Table 3 for the corresponding morphological traits.
+, ++ Estimate exceeds its standard error once or twice, respectively.

mance for the majority of traits indicate that extensive testcrossing programmes are essential in later stages of the hybrid breeding program. Significant SCA effects for sorghum grain yield had also been found by Jan-Orn et al. (1976), Singhania (1980), Bittinger et al. (1981), Hookstra et al. (1983), and Mishra et al. (1992).

In the present study, the repeatabilities for grain yield and related traits were highest in the two non-stress environments and lowest in the third and fourth highest yielding environments. These results suggest lower heritabilities under stress relative to non-stress conditions but do not imply a linear decline of heritabilities with increasing stress intensities. Similarly, heritability estimates were found to be slightly lower under stress conditions for grain yield in wheat (*Triticum aestivum* L.) (Ud-Din et al., 1992) and pearl millet (Bidinger et al., 1994), and independent of the stress intensity for grain yield of barley (*Hordeum vulgare* L.) (Ceccarelli et al., 1987; Ceccarelli, 1994).

Genotypes reacted differently to the growing conditions in the individual experiments, resulting in genotype × environment interaction variances larger than the genetic variances for major performance

traits. For improving grain yield in such variable target environments with large genotype × environment interaction effects, yield information from the whole range of possible environments should be involved in the definition of the selection criterion (Ceccarelli, 1987; Smith et al., 1990; Virk & Mangat, 1991; Ud-Din et al., 1992, Zavala-García et al., 1992a,b; Acevedo & Fereres, 1993; Moreno-Gonzáles & Cubero, 1993). An increased understanding of the environmental factors leading to large genotype × environment interaction effects is required to enable breeders to select representative test locations (Van Oosterom et al., 1996). Multi-year testing could be partially substituted by artificial creation of the appropriate stress factors with the aim to save time and reduce the sampling variation associated with the seasonal variation of the environmental conditions (Romagosa & Fox, 1993).

High grain yield was not related to early anthesis, indicating that the tested genotypes, with flowering dates between 57 and 77 days after planting, were phenologically adapted to the target area. Besides adequate phenology, osmotic adjustment of roots and shoots as well as optimum rooting depth and den-

sity are recommended selection traits in drought-prone areas (Ludlow & Muchow, 1990). Additionally, any trait is desirable that is shown to reduce lodging under terminal drought stress. It remains to be clarified whether stay-green is such a trait without a yield penalty (Ludlow & Muchow, 1990). Our results indicated a negative relationship between the number of green leaves at 95 days after planting and grain yield for hybrids. Furthermore, high grain yield was tightly genetically correlated with early drying up of the four lowest leaves in lines and hybrids. Rapid growth and, thus, high sink strength of the panicles of the highest yielding hybrids probably competed with the leaves for remobilizable nitrogen, leading to earlier senescence of the leaves. This may explain the fact that there was no advantage of the stay-green characteristic in the present study. On the other hand, delayed leaf rolling was found to be an easily measurable indirect selection trait with high heritability, and a moderate to tight genetic correlation to high grain yield. Delayed leaf rolling indicates the ability to maintain turgor despite drought stress, for instance through increased water uptake or osmotic adjustment (Blum, 1988). Since the photosynthetic capacity decreases with decreasing turgor (Martiniello, 1984), selection for delayed leaf rolling is recommended (Blum, 1988). However, Matthews et al. (1990) underlined that in the case of mid-season drought, high leaf rolling can be advantageous, and Corlett et al. (1994) showed that leaf rolling can offer protection from the effects of excess radiation, which may be a stress factor under extreme terminal drought (Acevedo & Fereres, 1993).

Conclusions

Hybrid breeding of sorghum could be a promising approach towards an improvement of sorghum grain yield in semi-arid areas of Kenya. In order to increase selection progress for major performance traits like grain yield, above-ground drymatter, and harvest index, the genetic variation in the gene pool of cytoplasmic-genic male sterile lines needs to be broadened. Furthermore, the resistance to lodging of heterozygous genotypes requires improvement before varieties are released. In traditional sorghum growing areas where the prepositions for successful hybrid seed production and marketing are not fulfilled, other types of variety could be produced which capitalize on heterozygosity, e.g., synthetic varieties.

Large genotype × environment interaction effects point to the necessity of evaluating breeding materials under a wide range of dryland conditions. In this process, time may be saved by artificial creation of the appropriate stress factors. The value of the stay-green character under terminal drought may depend on the materials under investigation.

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