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POTENTIAL OF WILD GERMPLASM FOR INCREASING YIELD OF GRAIN SORGHUM[1]

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INDEX WORDS

Sorghum bicolor, sorghum, virgatum, arundinaceum, verticilliflorum exotic germplasm, transgressive segregation, introgression, backcross

Sorghum [*Sorghum bicolor* (L) MOENCH] backcross populations containing 3 to 50% wild germplasm were evaluated in south central India for grain yield and nine related traits No individual BC_0F_2- to BC_3F_2-derived lines were high transgressive segregates for grain yield Only 1 5% of all BC_3F_2- or BC_4F_2-derived lines were transgressive segregates, with 26% higher mean grain yield than their respective recurrent parents The ten highest-yielding BC_2F_2- to BC_4F_2-derived lines per mating having parent CK60B yielded an average of 14% more than CK60B, which was, at the 5% level, a statistically significant difference However, the increased yield was associated with increased plant height The highest-yielding lines from RS/R/A2725 × virgatum and RS/R/A2725 × verticilliflorum were an average of 13 5% higher-yielding than RS/R/A2725 (a significant difference) and were equal in plant height Selection increased BC_2 mean grain yields by 6 to 27% Population mean yield, mean yield of selected lines, and frequency of high-yielding lines were highest in the BC_4.

INTRODUCTION

The species *Sorghum bicolor* (L.) MOENCH is large and diverse, containing both wild and cultivated races (DE WET, 1978). Genetic improvement of grain yield potential in grain sorghum has often involved the use of exotic but cultivated germplasm. However, much of the genetic diversity of the cultivated races has yet to be utilized in breeding

The wild sorghum races of Africa have not been used at all in breeding for grain yield. This is reasonable since these races have a very low grain yield and are agronomically very unsuitable. Natural introgression, which occurs extensively across Africa, played a part in the development of the crop (DOGGETT, 1965; DE WET et al., 1970), but today it apparently produces only troublesome weeds.

However, introgression of wild germplasm has been used in oats (*Avena sativa* L.) (FREY, 1976) and barley (*Hordeum vulgare* L.) (RODGERS, 1982) in Iowa, USA to increase grain yield by up to 40% over the recurrent parent. The usefulness of introgression in these two temperate cereals led us to examine its wider applicability by introgressing germplasm of three wild diploid sorghum races into two grain sorghum cultivars.

Sorghum is of tropical origin, and the studied populations were evaluated in the semi-arid tropical environment of south central India, providing an evaluation of introgression in a different genetic and environmental background. The objective was to predict the usefulness of wild sorghum for improvement of grain yield, and the optimal level of introgression (i.e., the optimal number of backcrosses) for obtaining superior lines.

MATERIALS AND METHODS

Experimental procedures

Genetic material. Each of two cultivated sorghum lines (herein called recurrent parents) was crossed with three wild sorghum accessions. The origins of the five parents are as follows. Combine Kafir 60B (CK) is a dwarf $(dw_1dw_1dw_3dw_3dw_4dw_4)$ inbred line developed in Texas, USA, from mainly kafir germplasm. RS/R line A2725 (RS) is an inbred line produced by the sorghum population improvement project at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India. RS is derived from an African population of mainly caudatum parentage. Each of the three wild parents represents a different wild race from Africa. The virgatum accession (VI) was collected in Egypt, the arundinaceum accession(AR) in the Ivory coast, and the verticilliflorum accession (SV) in the Republic of South Africa.

Several plants of CK and RS were hand-emasculated and crossed as females to several plants of each of the wild parents. Resulting BC_0F_1 (i.e., F_1) plants from each mating were (1) crossed to the recurrent parent and (2) self-pollinated to produce the BC_0F_2 (i.e., F_2) generation. In this and all subsequent backcrosses, bulk pollen from 2 to 50 BCF_1 plants was used to pollinate 5 to 10 hand-emasculated recurrent parent plants in each cross.

Backcrossing was continued in the same fashion (Fig. 1) until the BC_4F_1. From each backcross generation (BC_g, $g = 0...4$) of each of the six matings, 50 random BC_gF_2 plants were self-pollinated to produce 50 BC_gF_2-derived lines in the F_3. Each BC_gF_2-derived line was advanced to the F_4 by self-pollinating 10–20 F_3 plants and bulking the seed.

A set of 50 BC_gF_2-derived lines will herein be referred to as a population. A particular level of backcrossing will be called a generation. The study thus included 30 populations (6 matings × 5 generations) comprising in principle a total of 1500 lines.

Design and management of experiments. All experiments were conducted at the ICRISAT Center near Hyderabad, India, on deep vertisols. The BC_0, BC_1, and BC_2 generations of all matings were evaluated in the rabi (postrainy season) of 1980–81 and kharif (rainy season) of 1981 (herein referred to as R80 and K81, respectively). The BC_2, BC_3, and BC_4 generations of all matings were evaluated in kharif, 1982 (K82).

Table 1. Traits evaluated, abbreviations, experiments in which evaluated, units, and formulae for calculated traits.

Trait	Abbreviation	Season			Units	Formula
		R80	K81	K82		
Days to flower	FL	x[a]	x	x		
Plant height	HT	x	x	x	cm	
Panicle weight	PW			x	kg/ha	
Grain yield	GY	x	x		kg/ha	
Dry fraction	DF			x		
K82 grain yield	GY			x	kg/ha	$GY \times DF$
100-kernel weight	KW	x	x	x	g	
Kernels per plot	KN	x	x	x		$(GY \div KW) \times 60$
Wet stover yield	SYW			x	kg/ha	
Stover dry fraction	SF			x		
Stover yield	SY			x	kg/ha	$SYW \times SF$
Biological yield	BY			x	kg/ha	$SY + (PW \times DF)$
Harvest index	HI			x		$GY \div BY$
Panicle type	PT	x	x	x		
Threshing percentage	TP			x		$GY \div PW$

[a] Measured in the indicated experiment.

Table 2. Mean grain yield of each parent and of its progeny (BC_0–BC_4) over K81 and K82, and the number of high-yielding BC_2 to BC_4 lines produced by each parent.

Parent	Parent grain yield (kg/ha)	Mean progeny grain yield (kg/ha)	Number high-yield lines in K82[a]
Cultivated			
CK60B	4050	2910	16
RS	4560	2890	24
Wild			
Virgatum	130	3230	20
Arundinaceum	610	2820	8
Verticilliflorum	1380	2620	12

[a] Number of progeny lines included in the 40 highest-yielding BC_2 to BC_4 lines in K82.

Only 24 lines per mating of the BC_0 generation were evaluated in K81, due to elimination of shattering lines and larger plot size for the generation. In K82, CK × AR and CK × SV BC_4 populations contained 35 and 25 lines, respectively, because of insufficient seed production. Six other populations contained between 40 and 50 lines in K82. All BC_gF_2-derived lines were in the F_3 generation in R80 and in the F_4 in K81 and K82.

All three experiments, which included lines, parents, and checks, were grown as randomized complete block designs with two replicates each. The R80 and K81 experiments were in a split-split plot arrangement. Main plots were matings, subplots were generations, and (nested) sub-subplots were lines, parents, and three checks, CSH1

(hybrid), CSH6 (hybrid), and Ind. Syn. 387-1 (inbred cultivar). Three entries of recurrent parents along with one entry each of wild parents and checks were randomized within each subplot. The K82 experiment was in a split-plot arrangement with matings as main plots and lines of all three generations, parents, and checks as (nested) subplots. One entry of wild parents and three entries of checks were randomized within each main plot, along with 18 entries of CK or eight entries of RS. In all experiments, parent entries represented not single plants, but samples from bulk seed.

An experimental unit (sub-subplot in R80 and K81 and subplot in K82) consisted of two rows, each four meters long, with 10 cm between plants in the row and 75 cm between rows. There were two exceptions. Each sub-subplot in BC_0 subplots in K81 consisted of four rows of four meters each to provide a border since many BC_0F_2-derived lines were very tall and rangy when grown in kharif. Also, recurrent parent sub-subplots in BC_1 subplots in K81 were bordered since recurrent parents were generally shorter than BC_1F_2-derived lines.

The R80, K81, and K82 experiments were sown on November 2, 1980, July 1, 1981, and June 19, 1982, respectively, at the rate of 250 seeds per plot and thinned to the correct spacing at about 20 days after sowing. All fields were given a basal application of 80 kg N/ha and a sidedressing of another 40 kg N/ha about one month after sowing. P and K were present in nonlimiting amounts.

Traits. The evaluated traits are listed in Table 1. Days to flower was recorded as the number of days after sowing when at least 50% of the panicles in a plot had begun anthesis. Height was measured from the ground to the panicle tip and recorded as the mean of five, six, and six, competitive plants per plot in R80, K81, and K82, respectively. Panicle type was a visual rating (1 to 7) of the compactness and branch and internode length of the panicles in a plot, with 1 designating the most open and 7 the most compact panicle. Values 1 to 7 roughly corresponded to the designations 1, 2D, 3D, 3E, 4D, 4E, and 6, respectively, of HOUSE (1980).

All panicles were cut from each plot (or from the two center rows of four-row plots in K81), sun-dried, and machine-threshed; the grain was weighed to obtain grain yield. (In K82, the weight of panicles in each plot was taken before threshing.)

In K82, a 20 to 30 g sample of kernels was taken from each plot and weighed. Each sample was then oven-dried and weighed again. The ratio of dry to initial weight was recorded as grain dry matter fraction; 100-kernel samples were taken from dried

Table 3. Wild and cultivated parent means for eight traits.

Trait	Mean of wild parent	Mean of cultivated parents
100-kernel weight	0.63 g	2.14 g
Days to flower	57.8	50.3
Plant height	265 cm	171 cm[a]
Panicle type	1	7
Threshing percentage	45.9	82.0
Biological yield	3250 kg/ha	8040 kg/ha
Stover yield	1610 kg/ha	2060 kg/ha
Harvest index	22.3	61.2

[a] CK60B, 131 cm; RS 210 cm.

Table 4. Analyses of variance over the BC$_0$, BC$_1$, and BC$_2$ generations in two seasons (R80 and K81)

Source of variation	Degrees of freedom	Mean square			
		grain yield	100-kernel weight	days to flower	plant height
Replicates seasons	2	77.6**	0.013**	31.3**	1294**
Season (S)	1	291.2**	0.795**	580.8**	122010**
Matings (M)	5	136.3**	0.012	79.0**	619
S × M	5	6.5	0.027*	19.5**	800**
Error (a)	10	4.5	0.05	4.8	124
Generations (G)	2	669.3*	2.103**	81.9**	17761**
M × G	10	9.7**	0.024**	8.1**	830**
S × G	2	12.0**	0.142**	37.7**	5150**
S × M × G	10	2.7	0.008**	8.3**	494**
Error (b)	24	1.5	0.002	0.9	44
Lines (M × G)	693	84.5	0.219**	86.5	3185
S × (Lines/(M × G)	693	64.8**	0.110**	60.3**	1333**
Error (c)	1594	18.1	0.038	10.5	256.

* Significant at the 5% level; ** Significant at the 1% level.

Table 5. Analysis of variance of BC$_2$F$_2$-derived lines over K81 and K82.

Source of variation	Degrees of freedom	Mean square			
		grain yield	100-kernel weight	days to flower	plant height
Years (Y)	1	28624**	9.841**	414.2*	9798
Matings	5	1549**	1.968**	1041.3**	90186
Years × Matings	5	273	0.068	27.1	2015
Error (a)	10	137	0.261	122.7	1162
Lines (L)/Matings	293	111**	0.137**	27.9**	2343**
(L × Y)/Matings	286	46**	0.039	2.3	177
(L × Y)/CK × VI	48	27	0.016	1.8	87
(L × Y)/CK × AR	49	30	0.022	1.3	265
(L × Y)/CK × SV	49	61**	0.040	2.5	137
(L × Y)/RS × VI	43	70**	0.036	3.5	250
(L × Y)/RS × AR	48	45	0.067*	2.9	233
(L × Y)/RS × SV	49	44	0.053	1.7	96
Error (b)	596	34	0.039	2.6	261

* Significant at the 5% level; ** Significant at the 1% level.

samples. In K81 and K82, grain yield was corrected for weight of glumes in entries with adhering glumes.

In K82, all stover left in a plot after panicles were harvested was cut, sun-dried, and weighed to obtain wet stover yield. A two-culm sample was taken from each plot, weighed, oven-dried, and weighed again. The ratio of the second to the first weight was recorded as stover dry matter fraction.

The above traits and other traits calculated from them are listed in Table 1.

Statistical analyses. Genetic and phenotypic variance components within populations and experiments were computed as linear functions of appropriate mean squares.

For a given experiment, the least significant difference between the mean of a single line and its recurrent parent's mean was

$$\text{LSD} = t_{0.05} \sqrt{\frac{1}{2} + \frac{1}{2u}} \ \text{MS}_1$$

where $t_{0.05}$ is the tabulated value of t at the 5% level of significance for the appropriate degrees of freedom, u is the number of entries of the recurrent parent, and MS_1 is the intrapopulation mean square for error (c) in R80 and K81 and for error (b) in K82.

The least significant difference between the mean of ten lines and the recurrent parent mean was

$$\text{LSD} = t_{0.05} \sqrt{\frac{1}{20} + \frac{1}{2u}} \ \text{MS}_1.$$

Realized heritability for a trait within a BC_2 population was

$$H = \frac{(\overline{X}_{h2} - \overline{X}_2)s_{p1}}{(\overline{X}_{h1} - \overline{X}_1)s_{p2}}$$

where $(\overline{X}_{h1} - \overline{X}_1)$ is the difference between the 20% highest lines and the population mean in K81, $(\overline{X}_{h2} - \overline{X}_2)$ is the difference between the mean of the same set of lines and the population mean in K82, and s_{p1} and s_{p2} are the phenotypic standard deviations in K81 and K82, respectively.

RESULTS

Mean grain yields of parents and progeny are are compared in Table 2 using data only from K81 and K82, since yield expression in R80 was poor (see below). The mean grain yield of RS was higher than that of CK60B, but their progeny had virtually equal yields. Grain yields of wild parents were very low. Progeny of virgatum, the lowest-yielding parent, had the highest mean yield and included 20 of the 40 highest-yielding BC_2-BC_4 lines in K82. For all traits, wild and cultivated parents differed considerably, the wild parents being very inferior agronomically (Table 3).

Genotype × environment interaction. Mean grain yields over all lines in R80, K81, and K82 were 1450, 1870, and 3930 kg/ha, respectively. Grain yield in K82 was higher primarily because later backcross generations were evaluated. Grain moisture content evaluated only in K82, was generally 4% or less.

The BC_0, BC_1, and BC_2 generations were evaluated in R80, (rabi, i.e., November to March, 1980–81) and K81 (kharif, i.e., July to October, 1981). Typically for a rabi

Table 6 Percentage of BC_1F_2-derived lines exceeding the grain yield of the recurrent parent in each population

Generation	Mating					
	CK × VI	CK × AR	CK × SV	RS × VI	RS × AR	RS × SV
BC_0 [a]	0.0	0.0	0.0	0.0	0.0	0.0
BC_1 [a]	2.0	8.0	2.0	4.0	4.0	0.0
BC_2 [b]	4.0	14.0	4.0	14.0	0.0	0.0
BC_3 [c]	10.0	14.0	26.0	10.0	8.0	9.3
BC_4 [c]	27.5	42.9	32.0	16.7	6.7	2.0

[a] Evaluation in K81.

[b] Evaluation of means over K81 and K82.

[c] Evaluation in K82.

season, there was no rainfall during R80 and solar radiation was high. Night temperatures early in the season reached as low as 10 C and day temperatures during grainfilling reached as high as 38 C. In K81, rainfall was unusually heavy: 120 cm, compared with an average of 75 cm. There was heavy cloud cover on many days, and temperatures were moderate (21–33 C).

Interactions of seasons (R80 and K81) with lines, matings, and generations were highly significant for grain yield, 100-kernel weight, days to flower, and plant height (Table 4). Two exceptions were seasons × matings and seasons × matings × generations interactions for grain yield.

All populations were poorly adapted to the rabi environment, in which they segregated for two undesirable traits: prostrate, profusely tillering growth habit (inherited from the wild parents) and poor seed-set (inherited from RS). Both unfavorable expressions were responses to the cool nights of early rabi, and of course had deleterious effects on grain yield of lines in which they occurred. There also was severe drought during grainfilling in R80. None of these climatic conditions occurred in K81 or K82.

There was an average amount of rainfall in K82 (June to October, 1982) and less extensive cloud cover than in K81. Mean grain yield of BC_2 lines was 2470 and 3520 kg/ha in K81 and K82, respectively. There was no interaction between matings or lines and years (K81 and K82) for kernel weight, days to flower, or plant height of BC_2F_2-derived lines (Table 5). Line × year interaction for grain yield was significant in two matings, CK × SV and RS × VI. Mating × year interaction for grain yield was not significant.

Error variances for grain yield were heterogeneous among experiments, according to a Bartlett's Chi-square test (LE CLERG et al., 1962). A logarithmic transformation of the data did not remove the heterogeneity. This does not affect the conclusion that (line × year)/mating interaction was important only for grain yield in only two matings (Table 5), because heterogeneity of error variances inflates F values (LE CLERG et al., 1962). However, the highly significant (line × season)/mating interactions (Table 4) should be interpreted cautiously.

Magnitudes of interactions indicate that the relative performance of genotypes was much more consistent across years in kharif (Table 5) than it was between rabi and

Table 7. Numbers of lines in each grain yield class for the 18 populations evaluated in K82.

Mating	Backcross generation	Class midpoint, grain yield (100 kg ha)										
		15	20	25	30	35	40	45	50	55	60	65
CK × VI	2*	1	1	2	8	11	18	3	4	1		
	3*			1	3	7	12	16	10			
	4*			2	1		9	12	11	4		
CK × AR	2*	1	3	9	6	5	9	11	4	2		
	3			3	1	11	17	11	5			
	4				1	2	3	16	11	1	1	
CK × SV	2	5	5	6	4	8	13	4	4		1	
	3		2	2	2	9	10	11	9	2	2	
	4*		1	1		4	5	7	5	2		
									CK	47.1		
RS × VI	2			1	1	6	12	14	5	5		
	3				1	3	10	12	10	4		
	4*	2				6	10	13	10	7		1
RS × AR	2*	5	2	6	6	10	11	6	1			
	3		2	3	4	8	13	13	3	2	1	
	4			2	4	7	8	9	13	2		
RS × SV	2	1	2	9	6	5	12	11	3	1		
	3		1	1	1	9	10	12	4	2	2	1
	4				1	9	21	9	7	1		
									RS =	49.8		

* Significant negative skewness at 5% level.

Cultivated   x   Wild

$F_1 \rightarrow$ 50 F_2 plants $\rightarrow$ 50 Bc_0F_2 -derived lines in F_4

$Bc_1F_1 \rightarrow$ 50 Bc_1F_2 plants $\rightarrow$ 50 Bc_1F_2 -derived lines in F_4

Bc_2F_1 -

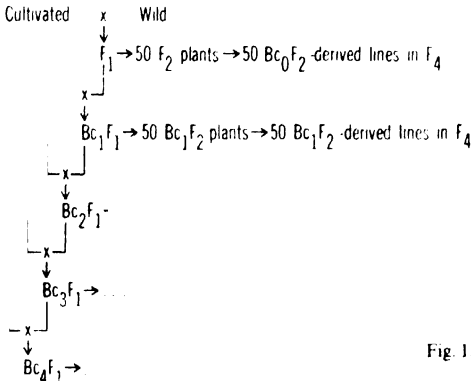$Bc_3F_1 \rightarrow$ ...

$Bc_4F_1 \rightarrow$

Fig. 1. Development of introgression populations.

kharif (Table 4). This was primarily due to the influence on two traits, seed-set and growth habit, of rabi conditions. Therefore, kharif results were used in evaluating the potential of introgressed material. This is appropriate, since most sorghum in the semi-arid tropics is produced in the rainy season (kharif).

Frequency of high-yielding progeny. Based on the K81 experiment, there were no BC_0

Table 8. Mean of the ten highest-yielding lines per mating for ten traits in K82, expressed as a percentage of the recurrent parents' mean.

Mating	KW[a]	FL	HT	PT	KN	TP	BY	SY	HI	GY
CK × VI	108	100	110*	96*	106	101	107	97	104	113*
CK × AR	92	101	120*	96*	132*	103*	113*	104	106*	114*
CK × SV	102	103*	141*	100	113*	98	118*	117	101	115*
RS × VI	104	96*	99	94*	116*	102	104	99	105	115*
RS × AR	104	100	104*	97*	105	102	102	101	102	108
RS × SV	99	111*	99	91*	113	101	107	100	103	112*

[a] Abbreviations in Table 1.
* Significantly different from 100 at the 5% level.

or BC_1 lines with a grain yield at least one LSD higher than the recurrent parent i.e., no high transgressive segregates). Five out of 50 lines in RS × VI-BC_2 were high transgressive segregates, based on K81, but, based on means over K81 and K82, there were no high-yielding lines in any BC_2 population. There were only eight high transgressive segregates based on K82 data, distributed as follows:

Mating	Generation	Number of lines
CK × VI	BC_4	2
CK × AR	BC_4	1
CK × SV	BC_3	2
RS × VI	BC_4	1
RS × SV	BC_3	2

These eight lines made up 1.5% of all BC_3 and BC_4 lines evaluated. The average yield advantage over the respective recurrent parents was 26%.

The frequency of transgressive segregation was low, in part because only very large differences were significant (average LSD's were 750 and 1000 kg/ha in K81 and K82, respectively). LSD's in turn, were large because only two replicates per experiment were used. However, an average of only 0, 3, 6, 13, and 21% of lines exceeded the respective recurrent parent's yield by any amount in the BC_0, BC_1, BC_2, BC_3, and BC_4, respectively (Table 6). The frequencies of lines given in Table 6 were unexpectedly low. For example, in the BC_4 of RS matings, made up of an average 97% RS germplasm, only 16.7, 6.7, and 2.0% of the lines from RS × VI, RS × AR, and RS × SV, respectively, exceeded the mean yield of RS (Table 6), whereas 19, 53, and 36%, respectively, were significantly lower-yielding.

Frequency distributions for grain yield in K82 (Table 7) show that the number of low-yielding lines decreased considerably with backcrossing, whereas the upper end of the range changed little. There are nine lines in the 5750–6800 kg/ha range, over 1000 kg/ha higher than the recurrent parents. In RS × VI, 17 lines yielded over 5250 kg/ha. One-third of the distributions had significant negative skewness.

The ten highest-yielding lines per mating in K82, regardless of generation, were evaluated for 100-kernel weight, days to flower, height, panicle type, kernel number, threshing percentage, biological yield, stover yield, harvest index, and grain yield (Table 8). The 30 lines selected from CK60B matings yielded, on average, 14% more

Table 9 Means in K82 of the 20% highest-yielding BC₂ lines per mating in K81, expressed as percent of the population mean.

Mating	Mean (% of population mean)										Realized heritability (GY)
	KWᵃ	FL	HT	PI	KN	TP	BY	SY	HI	GY	
CK × VI	98	100	103*	102*	107*	98*	104	80*	105*	108*	0.31
CK × AR	100	98*	93*	102*	117*	104*	104	93	108*	117*	0.56
CK × SV	112*	99*	106*	105*	120*	108*	109*	84*	119*	127*	0.70
RS × VI	103	99*	106*	78*	103	103*	97	92	106*	106*	0.37
RS × AR	105	92*	96*	93*	105	107*	92	71*	116*	111*	0.27
RS × SV	104	95*	98*	92*	108	104*	102	84*	113*	113*	0.36
Mean	104*	97*	100	95*	110*	104*	101	84*	111*	114*	0.43

ᵃ Abbreviations in Table 1.
* Significantly different from 100 at the 5% level.

than CK60B, a significant difference. However, the yield increases were associated with an average 24% increase in height. Biological yield averaged 13% greater than CK60B, compared with 3% for harvest index.

Lines from RS × VI yielded an average of 15% more than RS, with no change in height and a decrease in days to flower. They ranged in grain yield from 5480 to 6830 kg/ha, compared with 4980 for RS and 6210, 6170, and 5910 kg/ha for the checks Ind. Syn. 387-1, CSH6, and CSH1, respectively. Lines from RS × SV yielded an average of 12% more than RS (range: 5230 to 6440 kg/ha). They were significantly later than RS but equal in height. A yield difference of 8% in RS × AR was not significant.

There were no significant differences in kernel weight, but kernel number was higher in three matings. There were no significant differences in stover yield.

Response to selection. Realized direct and correlated response to selection was evaluated by choosing the 20% highest-yielding lines, based on K81, and taking their means for grain yield and nine other traits in K82 (Table 9). The average response to selection for grain yield was 14% of the BC₂ mean; however, selected lines yielded 12% less, on average, than their recurrent parents. Realized heritability for grain yield ranged from 0.27 to 0.70 (Table 9).

Selection for yield increased kernel number more than kernel weight, decreased stover yield, and increased harvest index and threshing percentage (Table 9). Changes in days to flower, height, and biological yield were relatively small and erratic. Thus, selection increased grain yield at the expense of vegetative production; selected lines were more 'cultivated'. Lines selected in RS × VI, however, had very open panicles (22% decrease in panicle type), compared with the population mean.

DISCUSSION

Frequency of transgressive segregation was 1% in the BC₂–BC₄ of sorghum introgressed populations, compared with 14 and 6.5% in oats and barley, respectively (LAWRENCE & FREY, 1975; RODGERS, 1982). The smaller effect of wild germplasm on favor-

able transgressive segregation for yield in sorghum may be due in part to a greater overlap between the wild and cultivated gene pools. Breeding populations and ancestral gene pools of North American oats and barley have been almost completely isolated from their respective wild progenitors, *A. sativa* and *H. spontaneum*, for thousands of years, whereas gene flow occurs continously between wild and cultivated sorghum in Africa (DOGGETT, 1965; DE WET et al., 1970). It is possible that over the history of the sorghum crop, most agriculturally useful wild genes have been incorporated into land races and cultivars through natural introgression and selection, despite roguing of hybrids.

However, the low frequency of transgressive segregates obtained in this study is consistent with theoretical studies. For example, BAILEY (1977) found that if the donor (wild) parent contributes the posivie allele at 12 out of 60 loci, the frequency of random BC_4 lines containing 50 positive alleles (2 more than the recurrent parent) is only $0.44''_0$. BAKER (1976) found that if the recurrent parent contributes 20 positive genes and the donor parent only one, the frequency of random progeny with 21 positive genes is $1.7''_0$ or less in any backcross. Therefore, large population sizes and efficient selection are necessary to recover a large number of superior lines from most introgressed populations.

There is evidence that genes for high yield were transferred from all wild parents (Table 8). The yield increases in RS × VI and RS × SV are most important for breeding purposes, because they were obtained in a superior genetic background; RS has much better grain quality, plant type, and grain yield than CK60B. Also, the high-yielding RS × VI lines were comparable in height to, and earlier than, RS. High yield of RS × SV lines may have been due in part to later maturity. The yield increases in CK60B matings may be largely attributable to increased height. However, 10 of the 30 high-yielding lines from CK60B matings were less than 140 cm tall, compared with 131 cm for CK60B.

Because BC_2F_2-derived lines in the F_4 were evaluated, many were highly heterogeneous, and single F_4-plant selections within superior lines could produce larger yield increases.

Few BC_0F_2- or BC_1F_2-derived lines even approached their recurrent parent's yield. Of the 60 high-yielding lines from Table 8, there were 10, 21, and 29 from the BC_2, BC_3, and BC_4 generations, respectively. LAWRENCE & FREY (1975) and RODGERS (1982) obtained the highest frequency of superior oat and barley introgressed lines in the BC_4.

Utilization of wild sorghum races. Wild relatives of crops are not obvious choices as sources of genes for high grain yield; certainly, the extensive, diverse, and largely unutilized gene pool of cultivated sorghum races is to be preferred. However, wild sorghum accessions, especially those collected outside the geographic and ecological range of the cultivated races, might contribute unique genetic factors with favorable additive or interactive effects. Race arundinaceum, for example, often grows in areas more humid than those used for grain sorghum cultivation; race virgatum often grows in drier areas. Their potential in breeding for stress environments is obvious.

Selection of wild parents based on their grain yields per se is probably ineffective. Virgatum was by far the poorest-yielding parent in this study, but its progeny included

the highest-yielding lines. In other matings, mean yield was lower than expected on the basis of parentage. Useful genes from wild sorghum races may be scarce; therefore, a long-term recurrent selection program will be ncessary to increase the frequency of desired genes from diverse wild accessions in an agronomically elite genetic background. Response to selection was demonstrated in this study. Base populations for selection should include no more than 12.5% wild germplasm, because of the deleterious effect on agronomic traits of large amounts of wild germplasm.

Only parallel, long term selection studies using introgressed and nonintrogressed populations will demonstrate whether or not wild sorghum races are sources of useful genes not available in the cultivated subspecies.

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