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Comparisons of methods for introgressing exotic germ plasm into adapted sorghum

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Abstract The incorporation of exotic germ plasm into breeding populations can broaden and diversify the genetic base of adapted genotypes. To more effectively utilize the genetic resources existing in *Sorghum bicolor* (L.) Moench, a rapid and efficient method of incorporating exotic genotypes into adapted populations is needed. Therefore, this study was conducted to compare the effectiveness of backcrossing to a broad-based population versus backcrossing to an inbred line for developing improved lines from adapted × exotic crosses. A wild sorghum, a cultivated landrace, and a converted sorghum line were crossed to an inbred line (CK60) and a broad-based population (KP9B). After two generations of backcrossing to the respective adapted parent, 50 F_2 lines were derived from each of the backcross generations of every mating and evaluated at three test environments. Backcrossing to an inbred line (CK60) gave fewer high-yielding segregates and generated less genetic variation than backcrossing to a population (KP9B). Also, the number of agronomically acceptable lines derived from each CK60 mating was fewer than that derived from the corresponding mating with KP9B. Overall, the use of a broad-based population as an adapted recurrent parent for introgressing exotic genotypes may provide good opportunities for developing suitable inbred lines from adapted × exotic backcrosses.

Key words Sorghum · Introgression methods · Exotic germ plasm

Introduction

Most sorghum breeding programs in the United States, which are geared towards rapid development of cultivars, use established lines and elite germ plasm in the development of breeding materials. This repeated process of using a limited number of elite lines as parents of crosses will tend to reduce the genetic variation of breeding populations. Schertz et al. (1990) demonstrated that the range of isozyme diversity was much greater in exotic sorghum accessions than among US adapted lines. Cox et al. (1988) and Duncan et al. (1991) pointed out that very few plant introductions appear in the pedigrees of publicly released sorghum inbred lines and commercial hybrids in the United States. Indeed, several exotic strains of sorghum have proven to be useful sources of genes for (1) broader adaption of the crop, (2) increased yield, (3) improved nutritional quality, and (4) resistance to diseases and insects (Cox and Frey 1984; Cox et al. 1988; Bramel-Cox and Cox 1989; Duncan et al. 1991).

To enhance the pool of genes accessible to sorghum breeders in the United States, exotic sorghum accessions have been preadapted mainly through the sorghum conversion program. However, the complete conversion of an exotic sorghum into a temperate, adapted inbred line is very time consuming (Dalton 1970). Thus, there is a critical need to investigate alternative methods that are less time consuming and more efficient for transferring beneficial alleles from exotic strains into US adapted germ plasm without substantially reducing the frequency of existing favorable alleles (Duncan et al. 1991). The development of an efficient introgression scheme may accelerate the use of exotic germ plasm for the improvement of both performance and diversity in sorghum (Bramel-Cox and Cox 1989).

The traditional introgression scheme uses an inbred line as an adapted parent for backcrossing (Lawrence and Frey 1975; Cox et al. 1984; Bramel-Cox et al. 1986; Eaton et al. 1986; Bramel-Cox and Cox 1989;

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Halward and Wynne 1991). However, Tanksley and Hewitt (1988) found a significant specific interaction between the function of an introgressed chromosomal segment from a wild species and the genetic background of cultivars. Several researchers also found specific inter-actions between the expression of introgressed genes from exotic strains and the genetic background of the adapted parents, mainly because of the presence of strong dominance or epistatic interactions (Cox et al. 1984; Frey et al. 1984; Eaton et al. 1986; Bramel-Cox and Cox 1989). Consequently, the use of a single inbred line as a recurrent parent may limit the potential for extracting favorable specific interactions between adapted and exotic genotypes because it provides a relatively constant genetic background for introgression. As an alternative to the traditional introgression approach, Bramel-Cox and Cox (1989) proposed the use of a broad-based population as an adapted recurrent parent for backcrossing. This approach may facilitate the transfer of useful quantitative traits from wild accessions and unadapted landraces into adapted germ plasm because it places each allele or combination of alleles derived from an exotic parent in a much broader genetic background. This, in turn, enhances the opportunities to extract favorable epistatic combinations from among the adapted and exotic germ plasm sources (Bramel-Cox and Cox 1989).

Although the population backcrossing scheme has been used in a sorghum breeding program (Bramel-Cox and Cox 1989), no empirical study has been conducted to evaluate the effectiveness of such an approach. The objectives of the study presented here were (1) to compare the effectiveness of backcrossing to a broad-based population versus backcrossing to an inbred line for developing improved lines and (2) to determine the influence of the degree of diversity of the exotic parents on the effectiveness of the introgression schemes.

Materials and methods

The six matings used in this study were derived from crosses between two adapted genotypes (CK60 and KP9B) and three exotic sorghum accessions ('12-26', 'Segeolane', and 'SC408'). CK60 is an adapted three-dwarf inbred line that contains a genetic male-sterile gene (ms_3ms_3) to facilitate crossing, and KP9B is a broad-based random mating population developed at Kansas State University using genetic male sterility (Zavala-Garcia et al. 1992). '12-26' is a wild sorghum of race virgatum, which was collected in Egypt, 'Segeolane' is a strain of race kafir cultivated in Botswana as a landrace, and 'SC408' is a conversion line derived from a caudatum-guinea landrace from Nigeria, which was released by the Texas Agricultural Experiment Station-USDA Conversion Program.

Bulk pollen collected from a sample of 5–10 plants of each exotic parent was used to pollinate 8–14 genetic male-sterile plants of CK60. A mixture of seeds from the resulting BC_0F_1 plants of each mating was sown for crossing to CK60 and for self-pollination to generate the BC_0F_2 generation. The BC_1F_1 and BC_2F_1 seeds of each mating were obtained by pollinating 10–12 genetic male-sterile plants of CK60, each with bulk pollen taken from 8–10 BC_0F_1 and BC_1F_1 plants, respectively. Over 100 male-fertile F_2 plants were harvested from each of the BC_0F_2, BC_1F_2, and BC_2F_2 generations of each mating.

Because of heterogeneity in KP9B, each plant derived from an exotic accession was crossed to a random male-sterile (ms_3ms_3) plant from KP9B to produce 22–36 plant-to-plant crosses (BC_0F_1). Each plant-to-plant cross was sown in a separate row for crossing to the adapted population and for self-pollination to generate the BC_0F_2. Each plant-to-plant cross was individually mated to random sterile plants of KP9B to form the 22–36 BC_1F_1 plants. A similar procedure was used to generate the BC_2F_1 plants. At least 10 male-fertile F_2 plants were harvested from each of the BC_0F_2, BC_1F_2, and BC_2F_2 generations of every plant-to-plant cross in each mating of KP9B. From the harvested plants, 50 random F_2 plants were drawn from each of the BC_0F_2, BC_1F_2, and BC_2F_2 within each of the six matings for testing in the F_3.

Each mating generation combination consisted of 50 F_2-derived lines and was referred to as a population. In 1990, a field trial that consisted of 6 BC_0 and 6 BC_1 populations was planted in Manhattan (Kan.). The 1991 experiment was comprised of 6 BC_1 and 6 BC_2 populations and was sown in both Manhattan and Garden City, Kan. An additional population which was composed of 60 random S_1 families from KP9B was included in each trial in both 1990 and 1991. The sets of random BC_1 lines tested in 1990 were different from those tested in 1991.

All experiments were conducted in a blocks-in-replication design with a split plot arrangement. Each experiment was replicated twice. The 13 populations (six matings × two generations + S_1 families) were randomly assigned to the main plots. The 50 F_2-derived lines from each population or main plot were split into two sets of 25 lines each. Each set of 25 lines, along with four rows of the adapted parent and one row of the exotic parent, were randomly assigned to the subplots of each block in the main plot. The sub-plot was a single row 6 m in length with 75 cm between rows.

All plots in Garden City were machine harvested; individual plot grain yields were recorded. In Manhattan, grain yield was obtained by hand harvesting plants from an area 1 m long and 75 cm wide in each plot. Days to flowering were recorded as the number of days from planting to the date when 50% of the plants in a plot were shedding pollen. After anthesis, plant height (cm) was measured as the distance from the soil surface to the tip of the panicle and was recorded as an average of 2–8 plants per plot depending on the uniformity of the test entry. A sample of 100 seeds was drawn from each plot to determine the seed weight.

Combined analyses of variance were calculated for each backcross population. Individual analyses were also computed for each population within a location by using the model of Schutz and Cockerham (1966). The difference between the mean yield of an F_2-derived line and its adapted parental mean yield in each population was tested by using Fisher's protected LSD (Ott 1988) with the standard error calculated from the individual analysis within a location error mean square. A transgressive segregate was defined as an F_2-derived line with a mean yield exceeding the mean yield of its adapted parent by at least one LSD ($P = 0.05$).

The difference between the mean yield of the top-yielding 10 lines out of 50 lines and the mean yield of the adapted parent was tested by using the least significant difference (LSD) with the standard errors calculated from the individual analysis within a location error mean squares. The formula of Cox et al. (1984) was used to calculate the LSD. Differences among parents were tested using an LSD with the standard errors calculated from error mean squares pooled over the 12 populations in each location.

The raw data for each trait were standardized, with a block mean of zero and standard deviation of one, to remove significant block effects, as suggested by Bramel-Cox et al. (1990). Analyses of variance pooled across the 2 backcross generations of each mating within a location were calculated using the standardized data. Replications, blocks, and lines were considered to be random effects. Genetic variance were estimated by equating the observed mean squares to expected mean squares (Schutz and Cockerham 1966) and solving for the appropriate component. Standard errors of the variance components were calculated using the procedure proposed by Anderson and Bancroft (1952).

Results

In the combined analysis of variance for grain yield, the location × line interaction was significant in 2 of the 6 populations of CK60 and in all 6 populations of KP9B (data not shown). Of the four test environments, the growing conditions were favorable only at Manhattan in 1990. The unfavorable growing environments, Manhattan (1991) and Garden City (1991), were characterized by severe midseason drought stress.

Mean grain yield of KP9B was either similar to or significantly higher than that of CK60 in each test environment (Table 1). These two adapted parents differed significantly ($P = 0.05$) for plant height but not for days to flowering. The differences among exotic parents were significant for all traits in each environment. The wild sorghum ('12–26') was significantly lower yielding, earlier flowering, and taller than CK60 and KP9B. The mean yields of 'Segeolane' and 'SC408' were either comparable to or higher than those of CK60 and KP9B in at least two test environments. 'Segeolane' 's lower yield in Manhattan (1991) resulted from the early killing frost that shortened its grain filling. However, these two exotic parents were taller and later flowering than CK60 and KP9B.

In most instances, the mean grain yields of the KP9B matings were either greater than or similar to the mean yields of the corresponding CK60 matings (Table 2). Mean yields of matings of 'Segeolane' and 'SC408' with both CK60 and KP9B were significantly greater than or similar to the mean yields of the respective adapted parent. The '12–26' matings gave the tallest and the earliest flowering plants among matings with both CK60 and KP9B.

Table 2 Means of the F_2-derived lines for matings within each backcross generation grown at Manhattan and Garden City (*KP* KP9B, *CK* CK60, *WS* 12-26, *SE* Segeolane, *SC* SC408)

Mating	1990		1991			
	Manhattan		Manhattan		Garden City	
	BC_0	BC_1	BC_1	BC_2	BC_1	BC_2
	Grain yield (Mg/ha)					
CK × WS	2.33**	4.16	3.66	3.43	2.39	3.68
CK × SE	5.71**	4.97	4.64*	4.20	3.21*	3.36*
CK × SC	5.11**	5.47	4.18	4.10	3.46*	3.73
KP × WS	2.24**	3.83*	3.62	3.27	3.84	3.95**
KP × SE	6.13*	6.13**	4.64	4.00	4.62	4.16*
KP × SC	5.17	5.68	4.19	3.86	4.09*	4.00**
	Plant height (cm)					
CK × WS	257**	170**	176**	120**	166**	115**
CK × SE	177**	126**	126**	102	118**	98
CK × SC	162**	134**	127**	120**	123**	115**
KP × WS	259**	192**	134**	116**	128**	116**
KP × SE	171**	158**	128**	118**	121*	116
KP × SC	142**	138**	127**	119**	118**	123**
	Days to flowering					
CK × WS	65**	68	56**	55**	63**	65**
CK × SE	69**	67	60*	59*	73	72
CK × SC	67	66	63**	63	74	70
KP × WS	66	66	61**	60	70	70
KP × SE	65	70**	60**	62**	72	71
KP × SC	66	67	61**	61**	71	70

*,** Significantly different from the adapted parent at $P = 0.05$ and $P = 0.01$ levels, respectively

Table 1 Means of the two adapted and the three exotic parents grown at Manhattan in 1990 and at Manhattan and Garden City in 1991

Parent	1990	1991	
	Manhattan	Manhattan	Garden City
	Grain yield (Mg/ha)		
CK60	4.32b[a]	3.89c	3.09b
KP9B	5.25c	3.84c	4.62c
12-26	2.47a	1.18a	1.93a
Segeolane	6.21d	1.80b	4.98c
SC408	6.11d	4.64d	3.42b
	Plant height (cm)		
CK60	112a	104a	99a
KP9B	126b	107b	111ab
12-26	286e	233e	216d
Segeolane	212d	158d	175c
SC408	145c	139c	128b
	Days to flowering		
CK60	66b	60b	72b
KP9B	66b	59b	71b
12-26	62a	55a	59a
Segeolane	82c	79d	80d
SC408	65b	67c	75c

[a] Means within a column followed by the same letter were not significantly different at $P = 0.05$ level using LSD

The genetic variance for grain yield was of similar magnitude in the 3 mating of KP9B but not in those of CK60 (Table 3). The genetic variances of all of the KP9B matings for yield and days to flowering generally were comparable to or higher than those of the corresponding CK60 matings. All KP9B matings had higher genetic variances for plant height than the corresponding CK60 matings in each test environment. The genetic variance for the three agronomic traits of each KP9B mating was generally similar to or greater than the corresponding genetic variance of the S_1 families of KP9B in the 2 years.

The frequency distributions of all of the lines from 2 backcross generations of each mating within a test environment are presented in Table 4. The number of low-yielding lines was similar in the corresponding KP9B and CK60 matings for Manhattan (1990) and Garden City (1991). The frequency of lines that exceeded the overall mean of the populations by at least one standard deviation was greater in the KP9B × 'Segeolane' and KP9B × 'SC408' matings than in the corresponding matings with CK60. At least 1 line derived from these introgressed populations fell into a higher yield class than the S_1 families of KP9B in each test environment.

Table 3 Genetic variance estimates of lines pooleld over two backcross generations of each mating and the S_1 families from KP9B for grain yield, plant height, and days to flowering for Manhattan and Garden City expressed in standard deviation units

Mating	1990	1991	
	Manhattan	Manhattan	Garden City
	Grain yield		
CK60 × 12–26	0.32 ± 0.14*	0.31 ± 0.10**	0.10 ± 0.10
CK60 × Segeolane	0.17 ± 0.12	0.20 ± 0.10*	0.24 ± 0.11*
CK60 × SC408	0.18 ± 0.12	0.07 ± 0.10	0.49 ± 0.12**
KP9B × 12–26	0.35 ± 0.13**	0.37 ± 0.10**	0.35 ± 0.09**
KP9B × Segeolane	0.46 ± 0.12**	0.54 ± 0.12**	0.46 ± 0.11**
KP9B × SC408	0.32 ± 0.11**	0.45 ± 0.11**	0.54 ± 0.12**
KP9B – S_1	0.38 ± 0.13**	0.14 ± 0.14	0.24 ± 0.14*
	Plant height		
CK60 × 12–26	0.34 ± 0.06**	0.27 ± 0.05**	0.20 ± 0.05**
CK60 × Segeolane	0.42 ± 0.08**	0.54 ± 0.09**	0.42 ± 0.07**
CK60 × SC408	0.54 ± 0.10**	0.69 ± 0.11**	0.67 ± 0.12**
KP9B × 12–26	0.54 ± 0.09**	0.60 ± 0.09**	0.58 ± 0.10**
KP9B × Segeolane	0.66 ± 0.11**	0.89 ± 0.14**	0.76 ± 0.12**
KP9B × SC408	0.78 ± 0.14**	0.86 ± 0.14**	0.80 ± 0.14**
KP9B – S_1	0.70 ± 0.15**	0.45 ± 0.15**	0.49 ± 0.14**
	Days to flowering		
CK60 × 12–26	0.72 ± 0.14**	0.60 ± 0.11**	0.36 ± 0.07**
CK60 × Segeolane	0.29 ± 0.10**	0.44 ± 0.08**	0.84 ± 0.13**
CK60 × SC408	0.60 ± 0.14**	0.76 ± 0.13**	0.72 ± 0.13**
KP9B × 12–26	0.46 ± 0.14**	0.92 ± 0.14**	0.68 ± 0.12**
KP9B × Segeolane	0.55 ± 0.11**	0.63 ± 0.10**	0.86 ± 0.14**
KP9B × SC408	0.68 ± 0.13**	0.73 ± 0.12**	0.88 ± 0.14**
KP9B – S_1	0.54 ± 0.14**	0.54 ± 0.16**	0.63 ± 0.16**

*,** Significantly different at $P = 0.05$ and $P = 0.01$ levels, respectively

Table 4 Frequency distribution of 100 F_2-derived line means from two backcross generations of each mating for grain yield expressed in standard deviation units for Manhattan and Garden City

Mating	Standard deviations						
	-3 to < -2	-2 to < -1	-1 to < 0	0 to < 1	1 to < 2	2 to < 3	> 3
	(%)						
	Manhattan 1990						
CK60 × 12–26	9	49	31	4	5	1	
CK60 × Segeolane	1	4	25	57	12	1	
CK60 × SC408	1	4	32	49	12	2	
KP9B × 12–26	7	55	26	8	4		
KP9B × Segeolane		3	14	46	24	9	4
KP9B × SC408		4	29	50	14	2	1
KP9B – S_1		2	17	57	22	2	
	Manhattan 1991						
CK60 × 12–26	5	18	50	20	6	1	
CK60 × Segeolane			33	53	11	2	1
CK60 × SC408		4	36	52	8		
KP9B × 12–26	8	24	34	31	3		
KP9B × Segeolane	4	12	26	27	19	9	3
KP9B × SC408	4	11	34	34	11	5	1
KP9B – S_1		5	38	47	10		
	Garden City 1991						
CK60 × 12–26	6	33	39	18	4		
CK60 × Segeolane	2	17	61	18	2		
CK60 × SC408		21	44	31	4		
KP9B × 12–26	5	11	29	35	19	1	
KP9B × Segeolane		8	22	33	23	11	3
KP9B × SC408	4	13	27	26	21	7	2
KP9B – S_1			13	60	27		

The proportion of transgressive segregates for grain yield averaged 8% for matings of CK60 and 10% for matings of KP9B (Table 5). Although transgressive lines occurred in all matings of the three exotic parents, most of them were derived from matings of the landrace ('Segeolane'), regardless of which adapted parent was involved. The mean yield of each transgressive line from a mating exceeded the mean yield of the respective adapted parent by more than 20%.

Table 5 Percentage of positive transgressive segregates for grain yield and agronomically desirable lines from each backcross generation of each mating grown at Manhattan and Garden City

Mating	1990		1991				
	Manhattan		Manhattan		Garden City		
	BC_0	BC_1	BC_1	BC_2	BC_1	BC_2	Average
	(%)						
CK60 x 12-26	0(0)[a]	0(0)	0(0)	4(0)	0(0)	8(4)	2(1)
CK60 x Segeolane	26(0)	16(16)	12(14)	0(14)	0(4)	22(16)	13(11)
CK60 x SC408	28(0)	0(4)	0(0)	0(2)	24(0)	10(6)	10(2)
KP9B x 12-26	0(0)	8(2)	8(4)	2(16)	6(4)	0(2)	4(5)
KP9B x Segeolane	22(4)	36(6)	16(40)	14(24)	12(24)	2(12)	17(18)
KP9B x SC408	8(6)	2(8)	20(30)	10(26)	4(14)	4(12)	8(16)

[a] Figures in parentheses are percent of agronomically desirable lines with grain yields at least 10% better than the adapted parent which fell within the range of means of the adapted parent for plant height, days to flowering, and 100-seed weight

Table 6 Mean grain yield, plant height, and days to flowering expressed as percentages of the adapted parent means for the 10 highest yielding lines of each mating in each backcross generation for Manhattan and Garden City

Mating	1990		1991			
	Manhattan		Manhattan		Garden City	
	BC_0	BC_1	BC_1	BC_2	BC_1	BC_2
	%					
	Grain yield					
CK60 x 12-26	87*	147**	125**	116**	119*	141**
CK60 x Segeolane	167**	150**	148**	133**	143**	127**
CK60 x SC408	169**	155**	126**	134**	164**	138**
KP9B x 12-26	68**	119**	118**	128**	111*	106
KP9B x Segeolane	145**	171**	169**	151**	132**	116**
KP9B x SC408	127**	151**	154**	142**	124**	114**
	Plant height					
CK60 x 12-26	240**	133**	148**	122**	147**	115**
CK60 x Segeolane	157**	114**	136**	98	117**	98
CK60 x SC408	146**	122**	122**	120**	119**	116**
KP9B x 12-26	213**	141**	130**	127**	98	100
KP9B x Segeolane	143**	147**	121**	143**	102	106**
KP9B x SC408	117**	113**	128**	124**	118**	112**
	Days to flowering					
CK60 x 12-26	101	112**	90**	90**	99	92**
CK60 x Segeolane	108**	106**	106**	103**	108**	104**
CK60 x SC408	102	100	104**	104**	104**	100
KP9B x 12-26	101	100	101	106**	105**	104**
KP9B x Segeolane	105**	114**	106**	103**	107**	106**
KP9B x SC408	107**	104**	102**	102**	111**	105**

*,** Significantly different from the adapted parent at $P = 0.05$ and $P = 0.01$ levels, respectively, using LSD

In addition to grain yield, other traits are important in introgressed populations. In our study, lines with mean yields that exceeded that of the adapted parent by at least 10% and which fell within the range of the mean of the adapted parent for plant height, days to flowering, and 100-seed weight were considered to be agronomically acceptable (Table 5). The proportion of lines that combined high yield with acceptable performance for other agronomic traits averaged 5% for CK60 matings and 13% for KP9B matings, mainly because of the high-yielding lines in CK60 matings being taller than the adapted parent. Of all CK60 matings, CK60 x 'Segeolane' consistently gave the largest number of agronomically acceptable lines. On the other hand, the frequencies of agronomically desirable lines were comparable in all KP9B matings, although there were fewer lines in the KP9B x '12-26' mating.

Mean yields of the top-yielding 10 lines of the KP9B matings were not always better in each location than those of the corresponding matings of CK60 (Table 6). In general, the lines derived from the 'Segeolane' and 'SC408' matings were higher yielding than those derived from the '12-26' matings, no matter which adapted parent was involved. The highest yielding 10 lines of the 2 '12-26' matings yielded significantly lower than the respective adapted parent in the BC_0. In most cases, the yield increase of the selected lines was associated with a significant increase in plant height and days to flowering.

Discussion

The genetic background of an adapted parent could affect the expression of genes from an exotic parent in adapted × exotic crosses because of the presence of strong dominance or epistatic interactions (Lawrence and Frey 1975; Eaton et al. 1986; Bramel-Cox and Cox 1989). Our study compared two introgression schemes, backcrossing to a population versus an inbred line, in which the adapted parent differed in its genetic potential to complement the exotic parent. Each locus was expected to be fixed at one or zero in the adapted inbred line (CK60). On the other hand, the broad-based random mating population, KP9B, was expected to have a large number of segregating loci each at an intermediate allelic frequency. The three exotic parents used in this study represented different levels of genetic diversity in sorghum plant introductions. The wild sorghum, '12–26', has a large number of undesirable traits, such as shattering, profuse tillering, extremely open small panicles, very narrow leaves, thin stems, and small seeds. The landrace sorghum, 'Segeolane', has unacceptable height and maturity for the United States, while the converted sorghum line, 'SC408', has been prebred for better adaptation in the United States.

Mean yields of lines derived from the KP9B matings generally were comparable to or better than those of lines from the corresponding CK60 matings. The recovery of higher mean yields from adapted × exotic backcrosses depended on the productivity of the exotic parents. Lines derived from matings of the two high-yielding exotic parents, 'Segeolane' and SC408', had acceptable means ($\geq$ adapted) for yield in all backcross generations, regardless of which adapted parent was involved. Lines from the BC_0 and BC_1 generations of 'Segeolane' and 'SC408' matings were later flowering and shorter than those from the 2 '12–26' matings.

The limited number of backcrosses used in this study restricted the inferences that could be made regarding the nature of gene action involved in controlling the three quantitative traits. However, because changes in the mean yield, plant height, and days to flowering with increased proportion of adapted germ plasm followed a similar trend in the corresponding matings of CK60 and KP9B, the gene action that conditioned these quantitative traits could be assumed to be similar in the backcross populations of the two recurrent parents. The rates of reduction or increase in grain yield, plant height, and days to flowering of the F_2 lines from each mating with increased level of backcrossing generally supported Dudley's (1982) theory that backcrossing more than once to the recurrent parent, irrespective of its genetic background, would only be advantageous when the two parents differed markedly for a trait.

In addition to improved mean performance, increased genetic variance within an introgressed population is an important predictor of the usefulness of adapted × exotic backcrosses for selection. Because additive genetic variance represents the primary source of genetic variability in sorghum (Maunder 1969), the bias from dominance and dominance types of epistasis included in our variance estimates would be very small at this level of inbreeding (F_3). The introgression of exotic germ plasm could increase the additive genetic variance in a backcross population by introducing unique alleles, which would increase the number of loci contributing to the overall additive variance of a trait, and by reducing the frequency of the favorable allele to an intermediate level (Falconer 1981). Because the corresponding backcross populations of the two adapted parents involved the same exotic strain, exotic parents contributed very little to the difference in genetic variance between CK60 and KP9B. Thus, the presence of a large number of segregating loci in the adapted population, KP9B, could account for the greater genetic variance in the KP9B matings (Table 3). Because different individual plants derived from KP9B were used for backcrossing, this genetic heterogeneity of the population would contribute significantly to the genetic variance within each KP9B mating. This was confirmed by the significant mean squares among the F_1 families used to derive the F_2 lines in the KP9B matings (data not shown).

Specific interactions between the adapted recurrent parents and the donor exotic accessions could influence the utilization of plant introductions, particularly when the value of the exotic germ plasm source may not be known prior to its utilization. This is the case for traits such as combining ability for grain yield. Thus, exotic accessions that produced very few agronomically desirable lines because of their unfavorable specific inter-actions with a single adapted inbred line would be eliminated from a breeding program. This interaction could occur irrespective of the adapted inbred line degree of agronomic eliteness. Evidence for these interactions can be seen in the 3 matings of CK60, whose differential genetic variance, positive transgressive segregates, and lines with agronomic acceptability depended upon the exotic parent used (Tables 3–5). These results indicate that the mating of CK60 with 'Segeolane' would have the greatest potential for parent line development, while '12–26' and 'SC408' would have a lower potential value.

The relative importance of the exotic parent in the KP9B matings was reduced, even though the '12–26' mating still had a lower potential. Thus, the use of a broad-based population will reduce the negative impact of specific interactions on the utilization of diverse sources of exotic germ plasm. It will also increase the opportunities to benefit from any positive interactions, as seen in the mating of KP9B with both 'Segeolane' and 'SC408' (Tables 3–5). The increased positive transgressive segregates for grain yield and agronomic acceptability will result in better short-term gain from the use of KP9B versus CK60.

Backcrossing to the broad-based population is analogous to backcrossing each plant sampled from an exotic parent to different inbred lines. Each random plant derived from the population and used for backcrossing has the potential of contributing additional alleles, and thus, maximizing the number of segregating loci. Consequently, backcrossing to a population places each allele or combination of alleles derived from an exotic parent in a much broader genetic background (Bramel-Cox and Cox 1989).

The population backcrossing scheme that was elaborated by Bramel-Cox and Cox (1989) could take advantage of favorable alleles controlling quantitative traits in both wild and cultivated exotic accessions better than the inbred line backcrossing scheme. This approach could identify superior segregates that might be of both immediate and long-term value to the sorghum breeder. In the short term, most of the improved inbred lines derived from the adapted × exotic backcross populations could be tested further as parents of hybrids. In the long term, the impact of methods to more efficiently utilize a wider range of exotic germ plasm for quantitative traits will be critical to improve the genetic gain in these traits within the fairly narrow adapted gene pool.

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