

A. Menkir · P.J. Bramel-Cox · M.D. Witt

Comparison of trait associations in adapted × exotic matings of sorghum developed by two introgression methods

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Abstract The association among six traits in the F₂ lines derived from adapted × exotic backcrosses of sorghum developed via two introgression methods was studied using principal component analysis. The first principal component defined a hybrid index in matings of the wild accession ('12-26') but not in matings of the cultivated sorghum genotypes ('Segeolane' and 'SC408'), no matter which adapted parent was used. This component accounted for 27–42% of the total variation in each mating. The 'recombination spindle' was wide in all matings of CK60 and KP9B, which indicated that the relationships among traits were not strong enough to restrict recombination among the parental characters. The index scores of both CK60 and KP9B matings showed clear differentiation of the backcross generations only when the exotic parent was the undomesticated wild accession ('12-26'). None of the distributions of the first principal component scores in any backcross population was bimodal. The frequency of recombinant genotypes derived from a mating was determined by the level of domestication and adaptation of the exotic parent and the genetic background of the adapted parent. Backcrossing to a population (KP9B) was found to be superior to backcrossing to an inbred line (CK60) to produce lines with an improved adapted phenotype.

Key words Trait associations · Introgression methods
Principal components

Introduction

The utilization of exotic germ plasm has become increasingly important to sorghum improvement programs in the United States. Exotic germ plasm has proven to be a useful source of favorable genes to improve overall productivity and tolerance to stress factors (Duncan et al. 1991). However, most landraces and all wild sorghum accessions contain undesirable alleles for height, maturity, and other traits that render direct use of plant introductions unsuitable in temperate areas. The presence of a strong correlation between desirable and undesirable traits may limit the recovery of suitable segregates from adapted × exotic crosses.

Anderson (1949) stated that progenies derived from an introgressed population represent only a small fraction of all possible trait combinations between parents. The progeny will fall on a narrow spindle that runs between the two parents. Goodman (1966) described three statistical techniques for measuring the width of this "recombination spindle". His analysis found that the spindle width was smaller in multigeneration families of *Gossypium* (cotton) crosses than in single-generation families, irrespective of the computational procedure used. Bramel-Cox et al. (1987) and Cox et al. (1985) used the eigenvalues of the first principal component to calculate a measure of spindle width in adapted × exotic backcross populations of pearl millet and sorghum. The recombination spindle in each mating of both species was found to be relatively wide. These results suggested that the recombination between the adapted and exotic parental traits was not strongly restricted. Their principal component score, which was the sum of the products of the eigenvectors and the corresponding standardized values for all traits showed a clear differentiation of the backcross generations in all cultivated × wild sorghums but only in one mating of pearl millet.

The genetic background of the adapted parent could affect the expression of genes from exotic parents in adapted × exotic crosses because of the presence of strong domi-

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A. Menkir · P.J. Bramel-Cox (✉)
Department of Agronomy, Kansas State University,
Throckmorton Hall, Manhattan, KS 66506, USA.

M. D. Witt
Southwest Kansas Research Extension Center, Garden City, KS
67846-9132, USA

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nance or epistatic interactions (Bramel-Cox and Cox 1989). In a related study, Menkir et al. (1993) found there was an advantage to using a broad-based population to introduce positive alleles for grain yield from a wide range of exotic germ plasm sources. Another consequence of using a population versus an inbred line could be in the trait associations in introgressed populations. Therefore, the objective of the study presented here was to compare trait associations in segregating generations of adapted \times exotic backcrosses developed using these two types of recurrent parents.

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 (*Sorghum bicolor* L. Moench) accessions ('12-26', 'Segeolane', and 'SC408'). These matings are also described in Menkir et al. (1993). CK60 is an adapted three-dwarf inbred line that contains a genetic male sterile gene (*ms₃ms₃*) to facilitate crossing, and KP9B is a broad-based random mating population developed by Kansas State University (Zavala-Garcia et al. 1992). '12-26' is a wild sorghum of ssp. *arundinaceum* race *virgatum* 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 was collected from 5 to 10 plants of each exotic parent and used to pollinate 8 to 14 genetic male-sterile plants of CK60. A mixture of seeds from the resulting BC₀F₁ plants of each mating was sown for crossing to CK60 and for self-pollination to generate the BC₀F₂. The BC₁F₁ and BC₂F₁ seeds were obtained by pollinating 10–12 genetic male-sterile plants of CK60 each with bulk pollen taken from 8 to 10 BC₀F₁ and BC₁F₁ plants, respectively, in each mating. Over 100 male-fertile F₂ plants were tagged and harvested separately from each of the BC₀F₂, BC₁F₂, and BC₂F₂ generations of each mating.

Because of heterogeneity in KP9B, each plant derived from an exotic accession was crossed to a random male-sterile (*ms₃ms₃*) plant from KP9B to produce the BC₀F₁. Each plant-to-plant cross was sown in a separate row for crossing to the adapted population and for self-pollination to generate the BC₀F₂. A total of 22–36 BC₀F₁ plants of all paired crosses were individually crossed to a random sterile plant of KP9B to form the BC₁F₁. A similar procedure was used to generate the BC₂F₁ plants. At least 10 male-fertile F₂ plants were harvested from each plant-to-plant cross of the BC₀F₂, BC₁F₂, and BC₂F₂ generation in each mating of KP9B.

From the harvested plants, 50 random F₂ plants were derived from each mating of both CK60 and KP9B for testing in the F₃. Each mating-generation combination consisted of 50 F₂-derived lines and was referred to as a population. In 1990, the field trial consisted of 12 populations (BC₀ and BC₁) and was planted in Manhattan (KS). The 1991 experiment was composed of 12 populations (6 BC₁ and 6 BC₂) that were grown in Manhattan and Garden City.

All experiments were conducted in two replications of a blocks-in-replication design with a split-plot arrangement. The populations were assigned randomly to the main plots. The 50 F₂-derived lines from each population were split into two sets of 25 lines each. Each set of 25 lines, along with four entries of the adapted parent and one entry of the exotic parent, were assigned randomly to the blocks in the main plot. Each plot was a single row 6 m in length and spaced 75 cm from the adjacent plots.

All plots were machine harvested in Garden City. In Manhattan, grain yield was determined by hand harvesting 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. A 100-seed sample was drawn from each plot and weighed (gm) to determine the seed weight. Panicle type was a visual score (1–7) of the compactness of a panicle based on the ratings of House (1980). A score of 1 represented the most open panicle and that of 7 represented the most compact panicle. The number of panicles per square meter was also counted in each plot.

The raw data from each trait were standardized, with a block mean of 0 and standard deviation of 1, to remove significant block effects, as suggested by Bramel-Cox et al. (1990). Means for the F₂-derived lines and their parents were calculated from the standardized data. To ensure that the mean of the adapted parent was higher than the corresponding mean of the exotic parent, any particular trait for which the mean of the exotic parent exceeded the corresponding mean of the adapted parent was multiplied by -1. Principal components were computed from the phenotypic correlation matrix (Jolliffe 1986) of (1) a combined array of BC₀F₂- and BC₁F₂-derived line means of each mating in 1990 and (2) a combined array of BC₁F₂- and BC₂F₂-derived line means of each mating averaged over two locations in 1991. The spindle width was calculated as $(k-r_1)/(k-1)$, where k and r_1 were the total number of traits included in the analysis and the eigenvalue of the first principal component (PC1), respectively (Cox et al. 1985). The PC1 score, an index score, was calculated for each line as the sum of the product of the eigenvector and the corresponding standardized value for each of the traits. The degree of multiple correlation among traits also was measured by Kendall's coefficient of concordance (Kendall and Gibbons 1990). This coefficient varies from 0 (no correlation) to 1 (perfect correlation). The distributional properties (skewness and kurtosis) of the first principal component scores for each population were tested according to the method of Snedecor (1946).

Results

The wild accession ('12-26') was significantly ($P < 0.05$) taller and earlier flowering and had a lower grain yield and

Table 1 Means of the two adapted and the three exotic parents averaged over two locations in 1990 and 1991

Parent	Grain yield (Mg/ha)		Head number	
	1990	1991	1990	1991
CK60	4.32	3.49	14	10
KP9B	5.25	4.23	15	10
'12-26'	2.47	1.56	42	30
'Segeolane'	6.21	3.39	14	10
'SC408'	6.11	4.03	15	10
LSD	0.29	0.28	1	1
	Seed weight (gm)		Days to flowering	
CK60	2.31	2.50	66	66
KP9B	2.24	2.34	66	65
'12-26'	1.44	1.64	62	57
'Segeolane'	2.65	2.28	82	80
'SC408'	2.44	2.50	65	71
LSD	0.07	0.02	1.4	1.0
	Plant height (cm)		Panicle type	
CK60	112	102	4.9	5.0
KP9B	126	109	4.1	4.2
'12-26'	286	224	1.0	1.0
'Segeolane'	212	166	5.0	5.0
'SC408'	145	134	3.6	3.0
LSD	13	23	0.35	0.1

Table 2 Eigenvectors of the first and second principal components for each mating, the proportion of the total progeny variance (r/k) explained by the two components, the spindle width (R), and coefficient of concordance (W) for 1990

Traits	'12-26'		'Segeolane'		'SC408'	
	CK60	KP9B	CK60	KP9B	CK60	KP9B
First component						
Yield	0.41	0.28	-0.09	0.46	-0.45	-0.48
Head number	0.46	0.49	0.60	0.07	0.36	0.21
Plant height	0.01	0.37	0.48	0.61	-0.16	0.52
Days to flowering	0.44	0.18	0.03	0.56	0.44	-0.51
Panicle type	0.44	0.60	-0.55	0.14	0.40	0.22
Seed weight	0.48	0.39	-0.32	0.29	-0.54	0.38
r/k	0.38	0.31	0.28	0.29	0.28	0.31
R	0.74	0.83	0.86	0.85	0.86	0.83
Second component						
Yield	-0.25	0.03	0.35	-0.44	-0.08	0.05
Head number	0.33	0.21	-0.16	0.76	0.15	-0.64
Plant height	0.77	-0.64	0.42	-0.08	0.73	0.37
Days to flowering	-0.25	0.64	0.76	0.17	-0.50	0.38
Panicle type	0.36	-0.19	-0.01	-0.15	0.42	0.54
Seed weight	-0.22	0.32	0.31	0.42	-0.14	0.13
r/k	0.23	0.23	0.24	0.22	0.23	0.22
Coefficient of concordance						
W	0.35**	0.28**	0.17	0.26**	0.17	0.14

** Significantly different from zero at $P = 0.01$

Table 3 Eigenvectors of the first and second principal components for each mating, the proportion of the total progeny variance (r/k) explained by the two components, the spindle width (R), and concordance coefficients (W) for 1991

Traits	'12-26'		'Segeolane'		'SC408'	
	CK60	KP9B	CK60	KP9B	CK60	KP9B
First component						
Yield	0.33	0.25	0.45	0.53	-0.44	-0.60
Head number	0.48	0.54	-0.32	0.03	0.01	-0.37
Plant height	0.31	0.43	0.35	-0.65	0.55	0.54
Days to flowering	0.38	0.36	0.41	-0.12	-0.47	0.32
Panicle type	0.51	0.50	-0.43	-0.06	0.34	0.33
Seed weight	0.41	0.29	0.46	0.52	0.40	0.04
r/k	0.39	0.42	0.30	0.27	0.35	0.30
R	0.73	0.70	0.84	0.88	0.78	0.84
Second component						
Yield	0.56	0.34	0.25	-0.43	-0.08	-0.15
Head number	-0.11	-0.17	0.64	-0.47	0.70	0.39
Plant height	0.61	0.06	-0.40	-0.11	-0.21	-0.28
Days to flowering	0.10	0.58	0.59	0.52	-0.03	0.52
Panicle type	-0.37	-0.02	0.09	0.29	-0.42	0.18
Seed weight	-0.41	-0.72	0.08	0.47	0.53	-0.66
r/k	0.21	0.19	0.24	0.24	0.22	0.22
Coefficient of concordance						
W	0.30**	0.34**	0.17	0.14	0.14	0.14

** Significantly different from zero at $P = 0.01$

smaller seeds on a greater number of heads with extremely open panicles than the two adapted parents (Table 1). The landrace ('Segeolane') was consistently later flowering and taller than CK60 and KP9B ($P < 0.05$). The converted sorghum line, 'SC408', had a maturity similar to that of the two adapted parents but was slightly taller with more open panicles. In 1991, both 'Segeolane' and 'SC408' had significantly ($P < 0.05$) higher yields than the adapted recurrent parent. Because of the adjustment in the mean, all

correlations among the F_2 -derived families would be expected to be positive if trait associations reflected those among the parents. If these associations were large within a mating, they would indicate linkage or pleiotropy among parental genes (Bramel-Cox et al. 1987; Cox et al. 1985).

As shown in Tables 2 and 3, the eigenvectors of the PC1 for each mating between the wild sorghum ('12-26') and CK60 or KP9B had large positive weights for most of the traits in both years. The only differences between these two

recurrent parents were in the magnitude of the eigenvectors for yield, plant height, and days to flowering in 1990 and only seed weight in 1991. The PC1 accounted for 31–42% of the total variability. The values for the spindle width were 0.70 or higher in the two matings of '12-26'. The second principal component (PC2) of the CK60 × '12-26' mating combined the CK60 characteristics for plant height, head number, and panicle type with the undesirable exotic characteristics for yield, days to flowering, and seed weight in 1990. In the KP9B × '12-26' mating, a high PC2 score was associated with the exotic parent characteristics of a greater number of heads, taller plants, and earlier flowering with the adapted parent trait of heavier seeds. These results differed for 1991, where the CK60 × '12-26' mating combined the CK60 characteristics of higher yield and shorter plant height with the '12-26' traits for more open panicle type and smaller seed weights. The high PC2 score of KP9B × '12-26' was associated with a higher yield than KP9B and earlier flowering and lighter seeds than '12-26'.

Kendall's coefficient of concordance (W), which measured the communality of rankings for the six agronomic traits, was significant in each mating of '12-26' in both years (Tables 2 and 3). However, the degree of multiple correlation among traits was quite low ($\bar{W} = 0.28\text{--}0.35$).

The eigenvectors of the PC1 for matings between 'Segeolane' and the two adapted parents differed in sign and magnitude within each year (Tables 2 and 3). In 1990, the eigenvectors of the PC1 for the CK60 × 'Segeolane' mating were large for head number and panicle type, for which the parents did not differ, and combined the adapted parents' characteristics for plant height with the exotic parents' desirable seed weight (Table 2). On the other hand, the high score for the PC1 of the KP9B × 'Segeolane' mating was associated with the lower yield and heavier seed of 'Segeolane' combined with the shorter stature and earlier flowering of KP9B. In 1991, the eigenvectors of the PC1 for the CK60 × 'Segeolane' mating had high positive weights for grain yield, plant height, days to flowering, and seed weight and high negative weights for two traits for which the parents did not differ, head number and panicle type (Table 3). The PC1 of the KP9B × 'Segeolane' mating combined high positive weights for yield and seed weight with high negative weights for plant height. This component accounted for only 27–30% of the total variation, which was reflected in values of over 0.80 for spindle width in each mating.

The PC2 of the CK60 × 'Segeolane' mating had high positive eigenvectors for yield, plant height, days to flowering, and seed weight in 1990, which were similar to the weights given these traits in the PC1 of KP9B × 'Segeolane' (Table 2). The high score for the PC2 of KP9B × 'Segeolane' was associated with higher yield, higher head number, and lighter seeds. In 1991, the PC2 of CK60 × 'Segeolane' combined high positive weights for yield, head number, and days to flowering with high negative weights for plant height (Table 3). The high score for PC2 of KP9B × 'Segeolane' was associated with lower yield, fewer heads, earlier flowering, compact heads, and heavier

seeds. This component accounted for 22–24% of the total variation. The coefficients of concordance (W) were not significantly different from zero for the two matings of 'Segeolane', except for the KP9B × 'Segeolane' mating in 1991 (Tables 2 and 3).

The eigenvectors of the PC1 for the mating between 'SC408' and the two adapted parents differed in sign and magnitude between years (Table 2 and 3). In 1990, the PC1 of the CK60 × 'SC408' mating combined the higher yield and seed weight of CK60 with high positive weights for head number, days to flowering, and panicle type for which the two parents did not differ (Table 2). The high scores for the PC1 of the KP9B × 'SC408' mating in 1990 and in the CK60 × 'SC408' mating for 1991 (Table 3) were associated with the higher grain yield and later flowering of 'SC408' plus the shorter plants of KP9B. However, the PC1 of the KP9B × 'SC408' mating in 1991 combined the lower yield of 'SC408' with the shorter plant height and earlier days to flowering of KP9B. This component accounted for only 28–35% of the total variation in each mating. The R values varied from 0.78 to 0.86 in all matings of 'SC408'.

In 1990, the PC2 of CK60 × 'SC408' had high positive eigenvectors for plant height and panicle type and high negative eigenvectors for days to flowering (Table 2). The high score for the PC2 of KP9B × 'SC408' was associated with fewer heads, shorter plants, earlier flowering, and compact heads. In 1991, the PC2 of CK60 × 'SC408' combined high positive weights for head number and seed weight with high negative weight for panicle type (Table 3). The high score for PC2 of KP9B × 'Segeolane' was associated with high head number, later flowering, taller plants, and lighter seeds. The variance of PC2 for the two matings of 'SC408' differed very little (22–23%). The coefficients of concordance (W) were not significantly different from zero for each mating of 'SC408' in both years (Tables 2 and 3).

The frequency distribution of the PC1 scores (index scores) for the adapted (A) and wild sorghum (E) parents and their F_2 lines are shown in Fig 1. The wild sorghum and each of the two adapted parents were located at the extreme opposite ends of the distribution of index scores in each mating. The PC1 described differences between trait associations of the adapted and exotic parents. The distribution of index scores for each backcross generation in the two '12-26' matings had different patterns with neither significant skewness nor kurtosis, except for the KP9B × '12-26' mating in the BC_1 (Table 4). None of the BC_0 and BC_1 lines from the CK60 × '12-26' or KP9B × '12-26' matings fell outside the range of their parents (Fig 1). Although the index scores of the BC_1 and BC_2 lines from the CK60 × '12-26' mating fell within the range of their two adapted parents, some BC_1 and BC_2 lines from the KP9B × '12-26' mating had component scores exceeding that of their adapted parent. The distribution of the index scores of the F_3 lines from the CK60 × '12-26' mating was shifted toward the adapted parent, showing an increased proportion of adapted germ plasm with backcrossing. A similar shift in the distribution of the index scores of the F_3 lines from

Fig 1 The frequency distribution of the first principal component (PC1) scores for the adapted (A) and wild sorghum (E) parents and their F₂ lines (class interval = standard deviation)

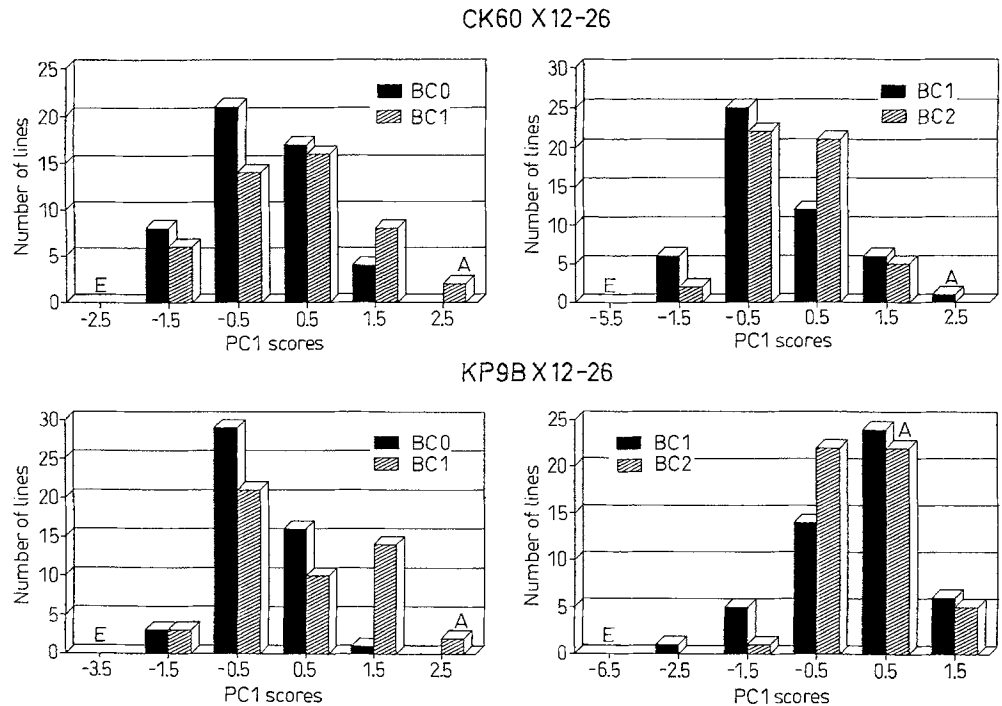


Table 4 The distributional properties of the first principal component scores for each mating in each backcross generation

Mating	BC ₀		BC ₁	
	Skewness	Kurtosis	Skewness	Kurtosis
	1990			
CK60 × 12-26	0.20	-0.52	0.30	0.14
KP9B × 12-26	-0.29	0.54	0.22	-0.77
CK60 × SEGEO	-0.17	-0.88	-3.49**	18.53**
KP9B × SEGEO	0.62	0.17	-0.42	-0.39
CK60 × 'SC408'	-0.57	0.79	-0.14	0.35
KP9B × 'SC408'	-0.01	-0.72	-0.72*	2.84**
	BC ₁		BC ₂	
	1991			
CK60 × 12-26	0.61	-0.30	0.03	-0.32
KP9B × 12-26	-0.83*	0.08	0.08	-0.49
CK60 × SEGEO	-0.77*	-0.04	-0.52	0.11
KP9B × SEGEO	-0.21	-0.74	0.16	-0.45
CK60 × 'SC408'	0.43	-0.16	-1.08**	3.28**
KP9B × 'SC408'	0.24	0.01	0.05	-0.66

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

the KP9B × '12-26' mating was observed from BC₀ to BC₁ but not as prominently from BC₁ to BC₂.

The frequency distributions of index scores for the adapted (A) and landrace sorghum (E) parents and their F₂ lines are shown in Fig 2. The PC1 scores better define the differences between 'Segeolane' and KP9B in 1990 (BC₀ versus BC₁) and between 'Segeolane' and CK60 in 1991

(BC₁ versus BC₂). The distributional patterns of the index scores for the two 'Segeolane' matings were different for each backcross generation. The index scores for CK60 × 'Segeolane' had a significant negative skewness and positive kurtosis only in the BC₁ (Table 4). Lines whose index score exceeded that of their adapted parent were found only in KP9B × 'Segeolane' matings (Fig 2). However, a few lines from both matings had index scores that fell below that of their exotic parent. The index scores for the two matings of 'Segeolane' showed some degree of differentiation between the BC₀ and BC₁ in 1990.

The frequency distributions of index scores for the adapted (A) and converted sorghum (E) parents and their F₂ lines are presented in Fig 3. The difference between the exotic and each of the adapted parents for the index scores was relatively smaller in these two matings, as would be expected given their relatively small mean differences for individual traits. Although the distribution of the index scores for the backcross generations seemed to have a similar pattern, particularly for the BC₀ versus BC₁ in both matings and BC₁ versus BC₂ for KP9B × 'SC408', it had a significant skewness and positive kurtosis only in the KP9B × 'SC408' mating in 1990 (Table 4). In the comparison of BC₁ versus BC₂ for CK60 × 'SC408', the difference in their distribution was due to a narrowing around the two parental classes. This was also seen in the significant values for skewness and kurtosis for the BC₂ lines from the CK60 × 'SC408' mating. The number of lines whose index scores fell below that of their adapted parent tended to be greater in CK60 × 'SC408', whereas the number of lines whose index scores exceeded that of their adapted parent was greater in KP9B × 'SC408'.

Fig 2 The frequency distribution of the first principal component (PC1) scores for the adapted (*A*) and landrace sorghum (*E*) parents and their F_2 lines (class interval = standard deviation)

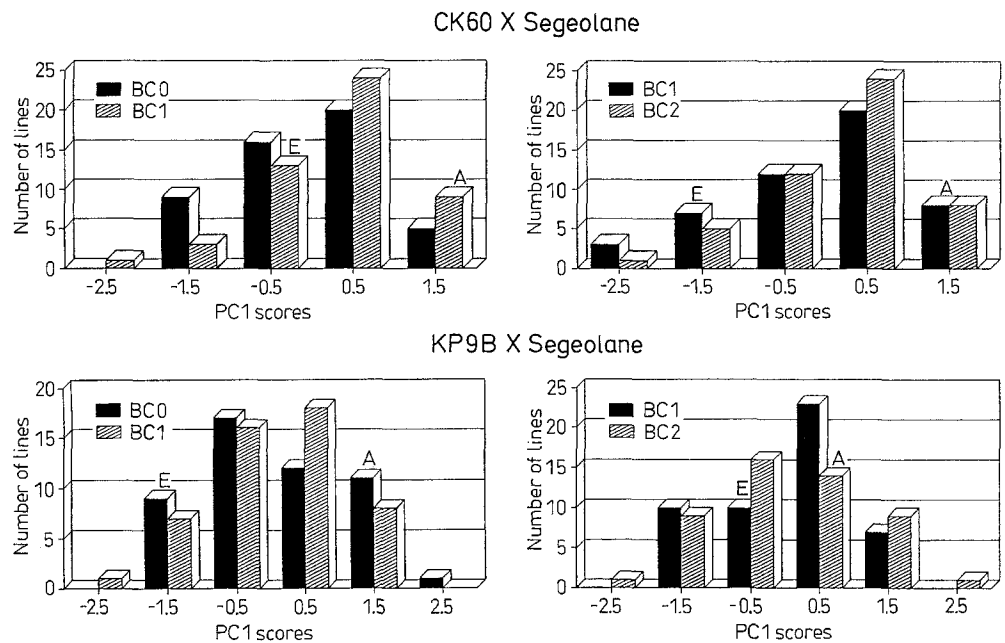
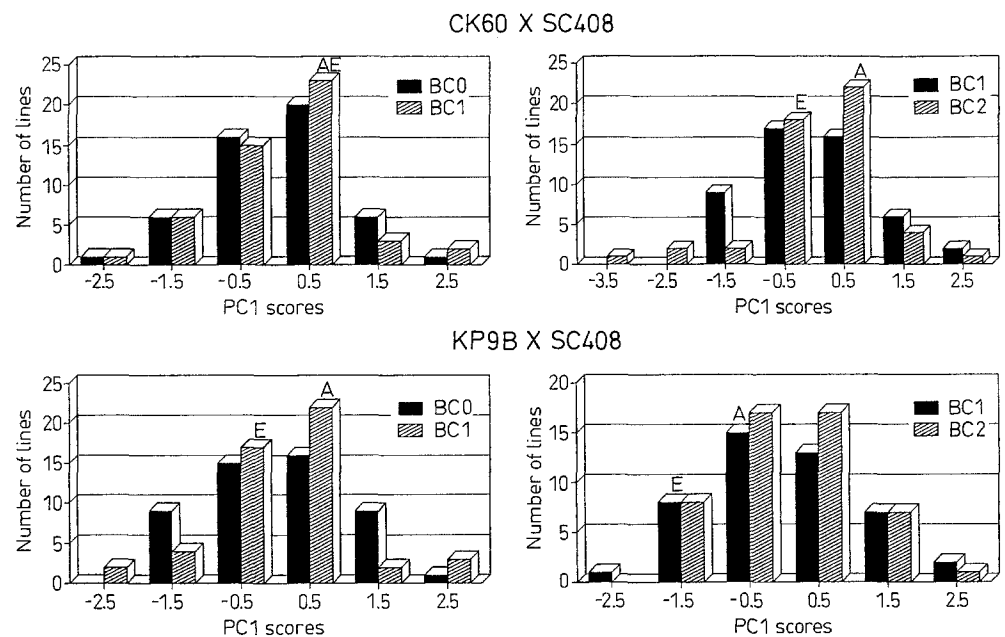


Fig 3 The frequency distribution of the first principal component (PC1) scores for the adapted (*A*) and converted sorghum (*E*) parents and their F_2 lines (class interval = standard deviation)



Discussion

According to Bramel-Cox et al. (1987) and Cox et al. (1985), the PC1 describes a “hybrid index” when it reflects a strong association between the phenotype of a progeny and that of either the adapted or exotic parent. The utility of this hybrid index could be strongly influenced by the degree of diversity between the two parents for the specific traits measured and by the specific test environment on the expression of these differences. The three exotic parents in this study differed in their level of diversity, as measured by the traits in the index, from the two adapted

parents. The greatest diversity was found in the matings involving the wild accession, ‘12-26’. The eigenvectors of the PC1 for matings between the wild accession (‘12-26’) and the two adapted parents (CK60 and KP9B) were all positive and large. Lines with a high positive index score would tend to be similar to the adapted phenotype, and those with high negative scores would tend to resemble the wild phenotype. Even though the PC1 defined a “hybrid index” in the two ‘12-26’ matings, the high values for the spindle width ($R = 0.70-0.83$) suggested that the relationships among traits were not strong enough to restrict recombination among parental characters. The small values

of the coefficient of concordance ($W = 0.28-0.35$) for each mating of '12-26' also confirmed that the recombination spindle was wide, no matter which adapted parent was involved (Goodman 1966).

The combination of traits that contributed greatly to the PC1 of each mating of 'Segeolane' and 'SC408' varied depending on the adapted parent and the test environments. The primary traits used to separate these two exotic parents from the adapted parents were yield, plant height, and flowering date in 1990, but only plant height and flowering date in 1991. The landrace, 'Segeolane', differed more than the preadapted 'SC408' for these traits. However, in both matings for 'SC408' and in CK60 × 'Segeolane' in 1990 and KP9B × 'Segeolane' in 1991, the PC1 was associated with a recombinant genotype that had characteristics derived from both the adapted and exotic parents. Therefore, this component did not describe a "hybrid index" in these matings, regardless of which adapted parent was involved. Even in CK60 × 'Segeolane' in 1991 and KP9B × 'Segeolane' in 1990, there was no indication of any associations that would interfere with recombination among parental characteristics.

The wild sorghum ('12-26') had characteristics of non-domestication, such as shattering, profuse tillering, extremely open small panicles, narrower leaves, thin stems, and smaller seeds. On the other hand, the two cultivated exotic accessions ('Segeolane' and 'SC408') were non-shattering with more compact and larger panicles on single stems, broader leaves, and larger seeds; a phenotype more closely related to the two adapted parents. Thus, the differences in the level of domestication of the exotic parents as measured by these traits seemed to affect the distribution of the PC1 scores in relation to the backcross generations. The index scores of both KP9B and CK60 matings should give a clear differentiation of the backcross generations when the exotic parent was the wild accession ('12-26'). This is consistent with the finding of Cox et al. (1985) and Goodman (1966) that a difference in gene frequency in the various backcross generations is the major source of the recombination spindle that existed in cultivated × wild crosses. The degree of differentiation between the backcross generations for the index scores became less clear in both the KP9B and CK60 matings when the exotic parents differed less, as seen with the cultivated sorghums ('Segeolane' and 'SC408').

The six traits included in our study represent important characters whose magnitudes define agronomic acceptability of progeny from adapted × exotic crosses. If different linkage blocks control these sets of traits in the exotic parent and the two adapted parents, the distribution of the PC1 scores of each mating would be expected to exhibit distinct groups in the backcross generations. However, none of the distributions tended to be bimodal because all significant values of kurtosis were positive in each mating of CK60 and KP9B (Darlington 1970).

The number of recombinant genotypes derived from a mating was dependent not only upon the differences in the level of domestication and adaptation of the exotic parent but also on the genetic background of the adapted parent.

Most of the F_2 -derived lines from the undomesticated wild sorghum ('12-26') mating were intermediate between the wild and any one of the two adapted parents (CK60 or KP9B). However, some lines from the KP9B × '12-26' and KP9B × 'Segeolane' matings exceeded the adapted parent for the index score in all three generations. The frequency of lines with index scores that fell outside the range of the two parents was quite large in the preadapted sorghum ('SC408') matings. This could have been due to the process of introgression or to the inadequacy of the traits to differentiate the parents in the PC1. Despite this, the number of lines whose phenotype was more adapted than that of their adapted parent were greater in the KP9B × 'SC408' mating than in the CK60 × 'SC408' mating. As suggested by Sneath (1976), interlocus and intralocus interactions of genes derived from both the adapted and exotic parents will contribute to the appearance of transgressive segregates. The higher frequency of transgressive segregates with an adapted phenotype in KP9B matings could have arisen from the contribution of a relatively higher number of plus genes from the population (KP9B) or greater opportunities for positive interactions because of a greater number of genes segregating in KP9B.

Even though the three exotic parents were different in their level of domestication and adaptation, our study found little evidence of the presence of a strong barrier to obtaining a desirable combination of parental characters with either CK60 or KP9B. The results of this study carried out in the temperate zone were similar to the findings from studies of Bramel-Cox et al. (1987) and Cox et al. (1985) on pearl millet and sorghum in the tropics. The number of lines derived from the matings of the wild parents whose phenotype exceeded that of the adapted parent was fewer than the number derived from matings of the cultivated exotic parents because of greater diversity. Generally, backcrossing to a population seemed to provide better opportunities for recovering improved phenotypes from adapted × exotic backcrosses.

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