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Trait Associations in Introgressed Populations of Sorghum[1])

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With 3 figures and 7 tables

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Abstract

Backcross populations from six wild × cultivated sorghum (*Sorghum bicolor* [L.] Moench) matings were evaluated for 100-kernel weight, plant height, tillers per plant, culm girth, panicle type, kernel percentage, kernel shape, kernel color, spikelet type, grain yield, kernel number, and days to flower. Of 43 correlation coefficients between quantitative characters, only 11 were greater than 0.20, and 5 were less than —0.20, indicating that any limitations on recombination between "wild" and "cultivated" traits were weak. First principal component eigenvectors, based on the first nine traits listed, were homogeneous in sign and accounted for 35 % to 49 % of the total variance across generations within matings, indicating a relatively wide "recombination spindle". Eigenvectors of first principal components within backcross generations were not homogeneous in sign and accounted for only 22 % to 32 % of the variation. Recombination spindles resulted more from differences in gene frequencies over backcrosses than from linkage or pleiotropy within backcrosses. Sorghum breeders should be able to obtain required associations of wild and cultivated traits with little or no hindrance due to reduced recombination between wild and cultivated chromosomes.

Key words: *Sorghum bicolor* — principal components — recombination — introgression — backcross

Trait associations are especially important in introgression of wild germplasm for crop improvement. Deleterious traits from wild relatives may be transferred to a crop along with useful ones, because of linkage or pleiotropy.

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Linkage will have larger effects in wild × cultivated than in other crosses if recombination frequencies are reduced owing to incomplete pairing of wild and cultivated chromosomes.

ANDERSON (1949) stated that only a small fraction of the total range of trait combinations will occur in introgression populations. For example, the distribution of introgression progeny for a set of three traits lies, according to ANDERSON (1949), within the narrow "recombination spindle" between the two parents indicated in *Figure 1*.

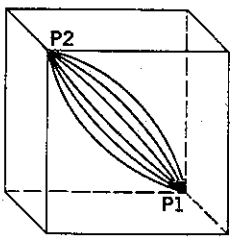

Fig. 1 The "recombination spindle" (ANDERSON 1949) between two parents P1 and P2 for three traits in three-dimensional space. Most progeny will be distributed within the spindle; few will lie in the corners of the cube

In studies of natural populations, sets of traits may be used to determine whether introgression between races or species has occurred. Linear combinations of traits, or "hybrid indices", may be used to determine the relative amounts of germplasm from the two parental races or species in each introgression progeny, and thus the distribution of progeny along the "recombination spindle". The index weight for each trait is "in proportion to its usefulness in demonstrating a known or suspected relationship" (HATHEWAY 1962). Weights may be assigned by dividing the traits of interest into two groups and creating two hybrid indices (one per group) by canonical analysis (HATHEWAY 1962). DOGGETT and MAJISU (1967) used a single index in a study of natural wild × cultivated sorghum hybrids, assigning weights according to each trait's proportional contribution to the overall correlation matrix.

This paper deals with the inverse problem, that is, determining for some set of traits whether a "recombination spindle" exists, given known parentages of individuals or lines. This problem is approached by using the first principal component score as a hybrid index and determining a) if the axis described by the first principal component is oriented with the two parents at its "endpoints", and, if so, b) how much of the total variation it accounts for (i.e., the width of the spindle). The data analysed are from a set of sorghum [*Sorghum bicolor* (L.) Monech] populations with known average proportions of wild germplasm. Results on genetic variability, genotype × environment interaction, and agronomic performance of individual traits in these populations were reported elsewhere (COX et al. 1984, COX and FREY 1984).

Materials and Methods

Genetic material

Six matings were produced by crossing each of two cultivated sorghum lines, CK60B and RS/R/A2725 (herein called recurrent parents), with three wild sorghum accessions.

Combine Kafir 60B (CK) is a three-dwarf 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 race caudatum parentage.

Each of the three wild parents represents a different wild race from Africa. The *Sorghum bicolor* spp. *arundinaceum* race virgatum accession (VI) was collected in Egypt, the *S. bicolor* spp. *arundinaceum* race arundinaceum accession (AR) in the Ivory Coast, and the *S. bicolor* spp. *arundinaceum* race verticilliflorum accession (SV) in the Republic of South Africa. All parents were relatively homogeneous and were considered homozygous.

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 (BC_g, $g = 0 \ldots 4$), bulk pollen from 2 to 50 BC_gF_1 plants was used to pollinate 5 to 10 hand-emasculated recurrent parent plants in each mating.

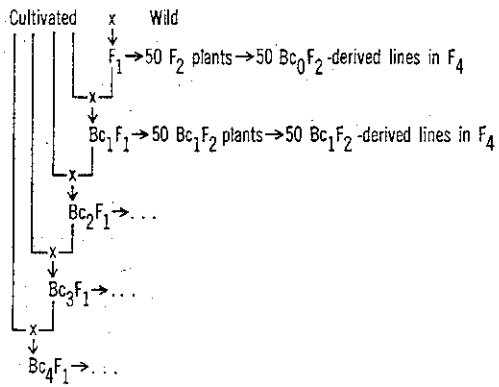

Fig. 2 Development of introgression populations

Backcrossing was continued in the same fashion (*Fig. 2*) until the BC_4F_2. From each backcross generation of each mating, 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 to 20 F_3 plants and bulking the seed.

A set of BC_gF_2-derived lines from a single generation of one mating 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).

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—1981 and the 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 the kharif, 1982 (K82).

All three experiments, which included lines and parents, 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 and parents. Three or more entries of the appropriate recurrent parent and one of the wild parent 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 plus parents as (nested) subplots. One to eighteen entries of parents were randomized within each main plot.

The R80, K81, and K82 experiments were sown on 2 November 1980, 1 July 1981, and 19 June 1982, respectively. 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. All plots 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 plots in BC_1 subplots in K81 were bordered, since recurrent parents were generally shorter than BC_1F_2-derived lines.

Traits

Traits measured in each season are listed in *Tables 1* and *2*. Date of flowering (FL) was recorded as the number of days after sowing when at least 50 % of the panicles in a plot had begun anthesis. Height (HT) was measured from the ground to the panicle tip and recorded as the mean of five, six, and six random, competitive plants per plot in R80, K81, and K82, respectively. Panicle type (PT) 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).

Tillers per plant (TL) was the mean number of panicle-bearing tillers on five random, competitive plants per plot. Culm girth (CG) was measured with a tape approximately halfway between the ground level and panicle on four random, competitive plants per plot.

Tab. 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	da	
Plant height	HT	x	x	x	cm	
Tillers per plant	TL	x			— —	
Culm girth	CG		x		mm	
Panicle type	PT	x	x	x	— —	
Grain yield	GY	x	x		kg/ha	GY x KP
Dry fraction	DF			x	— —	
K82 grain yield	GY			x	kg/ha	GY x DF x KP
100-kernel wt.	KW	x	x	x	g	
Initial 100-kernel wt.	KWI	x	x	x	g	
Kernel percentage	KP	x	x	x	— —	KW ÷ KWI
Kernels per plot	KN	x	x	x	1000s	(GY ÷ KW) x 6

[a] Evaluated in the indicated experiment

Tab. 2 Coded values of phenotypes for classificatory seed traits

Trait	Abbreviation	Coded value					
		0	1	2	3	4	5
Spikelet type	SP	Wild	Semi-wild	Interm.	Semi-cult.	Cult	— —
Kernel color	KC	Black	Dk.brown	Lt.brown	Red	Tan/pink	White/yellow
Kernel shape	KS	Elongate	Interm.	Round	— —	— —	— —

All panicles were cut from each plot (or from the two center rows of 4-row plots), sun-dried, and machine-threshed; the grain was weighed to obtain grain yield (GY). A sample of 100 kernels was taken from each plot of each experiment and weighed to obtain initial kernel weight (KWI). In some lines, glumes adhered to the kernels after threshing. Glumes were removed by hand from such samples, and the kernels were weighed a second time to obtain kernel weight (KW). For lines with nonadhering glumes, KW and KWI are the same.

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 (DF). One-hundred kernel samples were taken from oven-dried samples in K82. Other traits computed from the above traits are listed in *Table 1.*

Seed from R80 increase rows, which was used to sow the K81 experiment, also was used to assign coded values for spikelet type (SP), kernel color (KC), and kernel shape (KS) to BC_0, BC_1, and BC_2 lines (*Table 2*). "Wild" spikelet type indicates complete coverage of kernels by glumes; "cultivated" spikelet type indicates small, nonadhering glumes. For lines segregating for kernel color and shape, a mean, weighted by the approximate proportion of seeds falling into each class, was recorded.

Statistical analysis

Analyses were performed on BC_gF_2-derived line means within experiments for traits in *Table 1* and mean coded values for traits in *Table 2.* Phenotypic correlations were computed within populations and experiments.

Intramating and intrapopulation principal component analysis (KARSON 1982) was applied to BC_gF_2-derived line means ($g = 0 \ldots 2$). The first principal component is the linear function of a set of variables that has the maximum variance among all such linear functions (when the sum of the squared coefficients equals 1). In other words, it accounts for the maximum proportion of the variation in a population for a given set of variables. For each mating or population (generation within mating), the first principal component's vector of coefficients, or eigenvector, $E_{(t\times 1)}$, was found by solving the equations

$$E'E = 1,$$

$$\lambda_1 = E' \cdot R_{(t\times t)} \cdot E,$$

where R was the phenotypic correlation matrix of the set of variables being considered and λ_1 was the largest latent root of R. The percentage of variance accounted for by the first principal component was λ_1/t where t was the number of traits.

The vector of first principal component scores for a mating was computed as

$$Y_{(m\times 1)} = X_{(m\times t)} \cdot E_{(t\times 1)},$$

where X is the matrix of standardized means, x_{ij}, for t traits of m BC_gF_2-derived lines, and

$$x_{ij} = \frac{x_{oij} - \bar{x}_j}{s_j}$$

where x_{oij} is the raw mean of line i for trait j and $\bar{x}_j$ and s_j are the mean and standard deviation, respectively, for trait j within the mating.

The proportion of the intrapopulation variance accounted for by an *intramating* first principal component was V/t where V is the variance of H and

$$H_{(n\times 1)} = X_{(n\times t)} \cdot E_{(t\times 1)}$$

where there are n lines in the population and x_{ij} is computed as before, except that $\bar{x}_j$ and s_j are the mean and standard deviation, respectively, for trait j *within* the population.

Results and Discussion

Wild and cultivated parents differed considerably for all traits (*Table 3*). On the scales used, the wild parents had the higher means for days to flower (FL), plant height (HT), and tillers per plant (TL), and the lower means for all other traits. To give wild parents low values for all traits, the following three transformed variables were used in all analyses:

FLX = 100 — FL,
HTX = 400 — HT,
TLX = 10 — TL.

Mean intrapopulation phenotypic correlation coefficients for eight quantitative traits, including FLX, HTX, and TLX, are presented in *Table 4*. Entries lying above the diagonal are means over the BC_0, BC_1, and BC_2 generations of all six matings in R80 and K81. Entries below the diagonal are means over the BC_2, BC_3, and BC_4 generations of all matings in K82. Correlation patterns were similar in the two sets of generations; one exception was the correlation between grain yield and FLX, which was 0.54** in the BC_0—BC_2 and 0.15** in the BC_2—BC_4.

Tab. 3 Means of wild and cultivated parents for 12 traits

Trait	Mean of wild parents	Mean of cultivated parents
Grain yield[a]	710 kg/ha	4310 kg/ha
100-kernel wt.[a]	0.63 g	2.14 g
Days to flower[a]	57.8 da	50.3 da
Plant height[a]	265 cm	171 cm
Panicle type[a]	1	7
Tillers per plant[b]	4.9	1.1
Culm girth[c]	29.0 mm	43.5 mm
Spikelet type[d]	0	4
Shattering	Present	Absent
Kernel color[d]	0	5
Kernel shape[d]	0	2
Kernel fraction[c]	0.69	1.00

[a]Mean over K81 and K82
[b]Mean in R80
[c]Mean in K81
[d]See Table 2

Because the cultivated parents had high, and the wild parents low values for all traits, a positive correlation between two traits indicates that, in general, lines that are similar to one parent for one trait are similar to the same parent for the other trait. Thus, positive correlations imply a low level of recombination among traits; "recombination" in this context refers not to crossing over between linked genes, but to any occurrence of traits of both wild and cultivated parents in the same progeny line.

Tab. 4 Mean intrapopulation phenotypic correlation coefficients among 8 traits. Entries above diagonal are means over R80 and K81; those below the diagonal are from K82

Trait	Trait							
	GY	KW	KN	FLX	HTX	PT	TLX[a]	CG[b]
GY	–	0.36**	0.87**	0.54**	−0.04	−0.04	−0.19**	−0.23**
KW	0.41**	–	−0.07	0.32**	−0.02	0.06	−0.21**	−0.13**
KN	0.77**	−0.19**	–	0.45**	−0.05	−0.09**	−0.31**	−0.20**
FLX	0.15**	0.17**	0.05	–	0.15**	−0.15**	−0.08**	−0.38**
HTX	−0.03	−0.07	−0.01	0.19**	–	0.34**	−0.22**	−0.13**
PT	0.13**	0.04	0.04	−0.20**	0.35**	–	0.24**	0.17**
TLX	–	–	–	–	–	–	–	0.26**

[a] Recorded in R80 only
[b] Recorded in K81 only
** Significantly different from zero at the 1% level

Of 43 correlation coefficients in *Table 4*, there are 16 with absolute values greater than 0.20. Eleven are positive and five negative, indicating little restriction of recombination. Of the positive correlations, some, such as grain yield with kernel number (KN), have an obvious physiological basis, whereas others, such as panicle type with plant height (or its inverse, HTX), do not.

Principal component analysis within matings, based on nine traits for which wild and cultivated parents differed the most, was applied to BC_0, BC_1, and BC_2 lines (genotypes). Variation for TLX, culm girth, kernel percentage (KP), spikelet type, and kernel shape was virtually zero in the BC_3—BC_4, so those generations were omitted. If genotypes are assigned points in

Tab. 5 Eigenvectors of the first principal component in each mating, the proportion of total variance accounted for by the component (λ_1/k), and measure of spindle width, R

Trait	Mating					
	CKx			RSx		
	VI	AR	SV	VI	AR	SV
KW[a]	0.36	0.31	0.37	0.30	0.30	0.14
HTX[a]	0.38	0.38	0.41	0.07	0.39	0.35
TLX[b]	0.38	0.33	0.24	0.37	0.34	0.32
CG[a]	0.20	0.27	0.07	0.34	0.18	0.28
PT[a]	0.39	0.39	0.42	0.42	0.42	0.44
KP[a]	0.29	0.34	0.36	0.29	0.26	0.35
KS[b]	0.24	0.30	0.29	0.29	0.33	0.38
KC[b]	0.29	0.24	0.23	0.26	0.26	0.16
SP[b]	0.42	0.40	0.42	0.50	0.43	0.45
λ_1/k	0.49	0.46	0.46	0.35	0.42	0.41
R	0.58	0.68	0.68	0.73	0.65	0.66

[a] In K81
[b] In R80

nine-dimensional space according to their means for the nine traits, the first principal component defines an axis that minimizes the sum of the perpendicular distances from all points; it is the "long axis" of the nine-dimensional distribution. Eigenvectors (sets of coefficients of first principal-component scores) and percentage of total variance accounted for by the first principal component are presented in *Table 5*.

Principal components often cannot be interpreted biologically. In this situation, however, all elements of all eigenvectors are positive; therefore, component scores may be considered hybrid indices, because genotypes with relatively high means for most traits (more "cultivated" genotypes) will have high scores and genotypes with relatively low means ("wilder" genotypes) will have low scores. The distributions of genotypes in nine-dimensional space thus can be condensed into a single linear function, a hybrid index, that defines the "recombination spindle".

Proportion of total variance (λ_1/k) is an appropriate indicator of the width of the recombination spindle. The squared orthogonal distance (SOKAL 1961) between an observation and the first principal component is proportional to

$$\frac{1}{k-1} \sum_{i=2}^{k} c_{ij}^2,$$

where c_{ij} is the i^{th} principal component score of the j^{th} standardized observation. This is true because all principal components are uncorrelated. The mean squared distance over all observations is, then,

$$R = \frac{1}{n\,(k-1)} \sum_{j=1}^{n} \sum_{i=2}^{k} c_{ij}^2 = \frac{1}{n\,(k-1)} \sum_{i=2}^{k} n\lambda_i = \frac{k-\lambda_1}{k-1}$$

(because $\sum_{i=1}^{k} \lambda_i = k$). Since in this study the first principal component is a hybrid index, R is analogous to DEMPSTER's (1949) "recombination variance", a measure of spindle width, and ranges from 0, when λ_1 accounts for all variation, to 1 when no traits are correlated ($\lambda_1 = 1$). There is a negative linear relationship between R and λ_1/k; therefore, λ_1/k, which can range from 1/k to 1, measures spindle "narrowness". For the six matings, λ_1/k was between 0.35 and 0.49, meaning that spindle widths (R) were between one-half and three-fourths of maximum (*Table 5*). Other measures of spindle width are appropriate when the first principal component is not a hybrid index (GOODMAN 1966).

In the mating CK × AR (which is representative of all matings), the orientation of the hybrid index (first principal component) is determined to a great extent by differences between backcross generations (*Fig. 3*). (The second principal component in this case has no biological interpretation but is included only to produce a two-dimensional plot.) Index values of genotypes are closely related to the relative proportions of cultivated germplasm, i.e., backcross generations. This is consistent with the use of hybrid indices to determine the extent of introgression in studies of natural populations, and with GOOD-

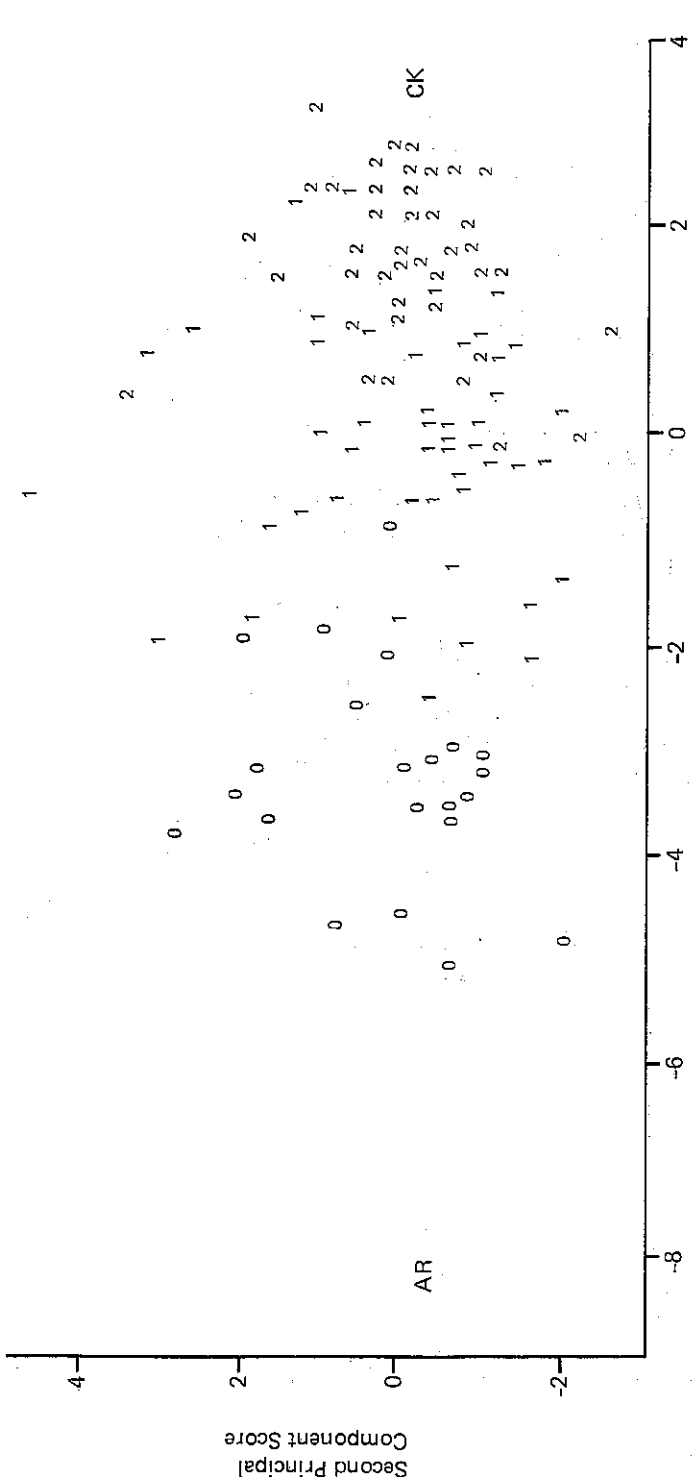

Fig. 3 Plot of first vs. second principal component scores for CK60B (CK), arundinaceum (AR), and their introgression progeny (0 = one BC_0F_2-derived line, 1 = one BC_1F_2-derived line, and 2 = BC_2F_2-derived line)

Tab. 6 Proportion of total variance within generations accounted for by hybrid indices corresponding to the eigenvectors in Table 5

Back-cross generation	Mating					
	CKx			RSx		
	VI	AR	SV	VI	AR	SV
0	0.17	0.19	0.21	0.19	0.20	0.19
1	0.14	0.18	0.24	0.14	0.24	0.26
2	0.16	0.16	0.25	0.15	0.16	0.20
Mean	0.16	0.17	0.23	0.16	0.20	0.22

MAN's (1966) finding that spindle width is smaller in multigeneration families of *Gossypium* crosses than in single-generation families.

On the basis of the hybrid index, lines within generations do not fall into distinct "wild-like" and "cultivated-like" groups (*Fig. 3*) as might be expected to happen if there were blocks of genes controlling complexes of wild traits. No intrageneration hybrid index distributions were significantly platykurtic, so there was no tendency toward biomodality. Correlations between the hybrid index and grain yield, a trait not included in the index, were small (0.04, 0.14, and 0.22 in the BC_0, BC_1, and BC_2, respectively).

Within generations, hybrid indices (linear functions containing coefficients from the across-generation first principal component) accounted for, on the average, only 19.5 % of the total variation (*Table 6*). Thus, the recombination spindle is more a result of different gene frequencies over backcross generations than of linkage or pleiotropy within generations. Eigenvectors of first principal components computed *within* populations (*Table 7*) were not homogeneous in sign, as were those computed across generations (*Table 5*). In no vector, however, were there more than three negative coefficients. There was little discernible pattern in the distribution of negative coefficients except, perhaps, that they were most common for kernel weight and kernel percentage. Intrageneration first principal components accounted for 21.8 to 32.1% of the total variance within generations of matings.

Table 7 shows that, even within generations, recombination of traits is not completely unrestricted. However, the present of negative coefficients and the smaller values of λ_1/k, as compared with across-generation analysis, indicate that the restrictions are not strong.

The nine traits included in the principal component analysis represent a wide range of plant and seed characters for which wild and cultivated sorghums differ considerably. The wild phenotype for most of the traits is agronomically undesirable, except under special conditions (for example, heavy rainfall, in which open panicles dry more rapidly). However, the degree of recombination among these traits is an indication of the general facility with which plant breeders can obtain desired combinations of wild and cultivated phenotypes.

Principal component analysis across generations indicated that few genotypes lie in the "corners" of the nine-dimensional space, that is, few progeny

Tab. 7 Eigenvector of the first principal components within populations and the percentage of total variance accounted for by the first principal component

Trait	CKxVI			CKxAR			CKxSV			RSxVI			RSxAR			RSxSV		
	BC_0	BC_1	BC_2	BC_0	BC_1	BC_2	BC_0	BC_1	BC_2	BC_0	BC_1	BC_2	BC_0	BC_1	BC_2	BC_0	BC_1	BC_2
KW	−.12	.40	.30	.19	−.43	−.36	.34	.41	.22	.50	−.44	.37	−.40	.19	.52	−.45	.19	−.38
HTX	.49	.21	.41	−.24	−.29	−.06	.42	.50	.43	−.17	−.11	.25	−.12	.40	.58	.33	.34	.43
TLX	.39	.31	.13	.02	.14	.25	.35	−.20	.29	−.22	.12	−.27	.11	.37	−.11	.33	.11	.08
CG	−.10	−.15	.12	.43	.52	.50	−.14	−.28	.12	.36	.42	−.10	.44	.10	−.12	.36	.30	.56
PT	.35	.21	.44	.08	.32	.41	.47	.21	.52	.24	.31	.40	.31	.21	.21	.29	.44	.50
KP	.13	.47	.22	−.19	−.44	−.35	.39	.49	.44	.30	−.47	.44	−.34	.46	.49	−.31	.42	.03
KS	.39	.29	.33	.46	.10	.01	−.31	.07	−.04	.40	−.29	.31	.20	.36	.13	.13	.38	.21
KC	.42	.34	.26	.51	.34	.51	−.02	.07	.27	.39	.44	−.23	.42	.08	.19	.50	−.07	.05
SP	.34	.46	.50	.45	.13	.01	.33	.41	.35	.30	.10	.48	.43	.51	.16	−.08	.48	.21
	Proportion of total variance																	
	.27	.28	.28	.32	.25	.24	.31	.30	.28	.26	.25	.22	.29	.26	.21	.30	.30	.24

contained all or most cultivated alleles for some traits and all or most wild alleles for others. This would be expected when most traits being considered are quantitatively inherited. In such a situation, the probability of recovering a parental genotype for one trait is low, and the probability of obtaining the complete genotypes of different parents for each of several traits is extremely low, even without pleiotropy or linkage between genes affecting different traits.

Intrageneration analyses gave no evidence of strong obstacles to recombination of traits, the set of traits used being comprehensive and the wild parents very diverse, both racially and geographically. These results are more applicable to improvement of quantitative traits such as grain yield, which may be affected by genes scattered throughout the genome, than to transfer of disease resistance, which may be governed by a single allele fortuitously linked to an allele with a deleterious effect on some other trait. Correlations between grain yield and the hybrid index, or between grain yield and individual traits other than yield components, were negligible. Therefore, grain yield could be improved independently of "wild" or "cultivated" trait complexes.

Zusammenfassung

Merkmalsassoziationen in Kreuzungspopulationen von Sorghum

In Rückkreuzungsgenerationen von sechs Populationen (zwei Kulturformen × drei Wildformen von *Sorghum bicolor*) wurden die Eigenschaften 1000-Korngewicht, Pflanzenhöhe, Bestockung, Halmumfang, Rispentyp, Kornanteil, Kornform, Kornfarbe, Ährchentyp, Kornertrag, Kornzahl und Blütezeit untersucht. Von 43 Korrelationskoeffizienten zwischen quantitativen Eigenschaften waren elf größer als 0,20 und fünf kleiner als —0,20. Für jede Population wurden zwei Arten von Hauptkomponenten berechnet, die jeweils auf den ersten neun Eigenschaften basierten: 1. Über alle Rückkreuzungsgenerationen und 2. für jede Generation getrennt. Im ersten Fall wurden zwischen 35 und 49 % der Gesamtvarianz erklärt und alle Elemente der entsprechenden Eigenvektoren waren positiv (*Tab. 5*). Sie zeigten eine relativ weite „Rekombinationsspindel" an. Im zweiten Fall wurden nur 22 bis 32 % der Gesamtvarianz erklärt, und die Elemente der Eigenvektoren waren teilweise negativ. Die Rekombinationsspindeln sind eher auf Differenzen in den Genfrequenzen zwischen den Rückkreuzungen als auf Kopplung und Pleiotropie innerhalb der Rückkreuzungen zurückzuführen. Es sollte in der *Sorghum*-Züchtung möglich sein, erwünschte Assoziationen zwischen Wild- und Kultursorteneigenschaften zu erhalten.

References

Anderson, E., 1949: Introgressive Hybridization. New York: John Wiley and Sons.

Cox, T. S., L. R. House, and K. J. Frey, 1984: Potential of wild germplasm for increasing yield of grain sorghum. Euphytica 33, in press.

— —, and K. J. FREY, 1984: Genetic variation for grain yield and related traits in sorghum introgression populations. Theor. Appl. Genet. 68, 145—153.

DEMPSTER, F. R., 1949: Effects of linkage on parental-combination and recombination frequencies in F_2. Genetics 34, 272—284.

DOGGETT, H., and B. N. MAJISU, 1967: Disruptive selection in crop development. Heredity 23, 1—23.

GOODMAN, M. M., 1966: Correlation and the structure of introgressive populations. Evolution 20, 191—203.

HATHEWAY, W. H., 1962: A weighted hybrid index. Evolution 16, 1—10.

HOUSE, L. R., 1980: A guide to sorghum breeding. ICRISAT, Hyderabad, India.

KARSON, M. J., 1982: Multivariate Statistical Methods. Ames, Iowa/USA: The Iowa State University Press.

SOKAL, R. R., 1961: Distance as measure of taxonomic similarity. System. Zool. 10, 70—79.

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