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Genetic variation for grain yield and related traits in sorghum introgression populations *

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Summary. Each of two sorghum (*Sorghum bicolor* (L.) Moench) cultivars were crossed with representatives of three wild sorghum races. Backcross-derived sorghum populations containing 3.125 to 50% wild germplasm were evaluated for grain yield, 100-kernel weight, days to flower, and plant height. Population means increased linearly with backcrossing for kernel weight, increased curvilinearly for grain yield, decreased curvilinearly for plant height, and changed erratically for days to flower. For all traits, the relationship between genetic variance and level of backcrossing deviated significantly from that expected based on an additive model. Genetic variance usually reached a maximum in the BC_1 or BC_2. The BC_1 genetic variance for grain yield, averaged over matings, was twice as large as the average BC_0 genetic variance. An epistatic model involving gene regulation is proposed as a plausible explanation for the results.

Key words: Backcross – Exotic germplasm – Wild germplasm – Epistasis – Genetic regulation

Introduction

Introgression of wild germplasm in cereal grains for yield improvement is an extreme example of a "high × low" cross (Langham 1961). Theoretical and computer simulation studies of crosses between two parents, one of which is inferior, have shown that one to three backcrosses increase the frequency of superior progeny (Bailey 1977; Baker 1976; Dudley 1982; Reddy and Comstock 1976).

Theoretically, the means of selfed populations derived from backcrosses to the superior parent increase linearly with percentage recurrent parent germplasm in the absence of epistasis. Genetic variances decrease nonlinearly when more than one plant is used to make each backcross and linkage and epistasis are absent (Cox 1984).

Empirical introgression studies in oats (Lawrence and Frey 1976) and barley (Rodgers 1982) showed that mean grain yield increased linearly with backcrossing but that, in some matings, genetic variances were unexpectedly high in the BC_1F_2 and later generations when compared with the F_2. As a result, the highest frequency of superior lines occurred in the BC_4 in both studies. Lawrence and Frey (1976) suggested additive × additive epistatic interactions and breakage of repulsion-phase linkages as possible causes of the elevated genetic variances in backcrosses.

The optimum population for variety development is one with a high mean and a large genetic variance. The purposes of this study were to (1) characterize sorghum (*Sorghum bicolor* (L.) Moench) introgression populations using means and genetic variances, (2) compare these with their expected values, and (3) investigate any deviations with regard both to genetic causes and consequences for utilization of wild germplasm.

Experimental procedures

Genetic material

Six matings were produced by crossing each of two cultivated sorghum lines, 'Combine Kafir 60B' (CK) and 'RS/R/A2725' (RS), with three wild sorghum accessions. CK is a three-dwarf inbred line developed in Texas, USA, from mainly South African kafir germplasm; RS is an inbred line of mainly race caudatum parentage produced by the sorghum population improvement project at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) near Hyderabad, India.

Each of the three wild parents represents a different wild race of 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.

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Several plants of CK and RS were hand-emasculated and used as females in crosses to several plants of each of the wild parents. Resulting F_1 plants from each mating were crossed to the recurrent parent, and self-pollinated to produce the F_2 (BC_0F_2) generation. In this and all subsequent backcrosses, bulked pollen from 2 to 50 BC_gF_1 plants was used to pollinate 5 to 10 hand-emasculated recurrent parent plants in each mating.

Backcrossing was continued in the same fashion (Fig. 1) until the BC_4F_2. From each backcross generation 1 to 4 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 ($g = 0 \ldots 4$) 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 mating-generation combination will be referred to as a population, and levels of backcrossing will be called generations. Thus, the study included 30 populations (6 matings × 5 generations).

Design and management of experiments

Both experiments were conducted at the ICRISAT Center near Hyderabad, India, on deep vertisols. The BC_0, BC_1, and BC_2 generations of each mating, comprising 24, 50, and 50 lines, respectively, were evaluated in the *kharif* (rainy season) of 1981 (herein referred to as K81). The BC_2, BC_3, and BC_4 generations of each mating, each comprising 50 lines, were evaluated in *kharif*, 1982 (K82).

Both experiments (K81 and K82), which included lines and parents, were grown as randomized complete-block designs with two replicates each. The K81 experiment was in a split-split plot arrangement. Main plots were matings, subplots were generations, and (nested) sub-subplots were lines, parents, and checks. Three entries of the appropriate recurrent parent and one entry 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, parents, and checks as (nested) subplots. For CK60B matings, 18 entries of CK60B and one entry of the wild parent were randomized within each main plot. For RS matings, only eight entries of RS were used. In both experiments, parent entries did not represent single plants, but were taken from bulked seed.

The K81 and K82 experiments were sown on 1 July 1981 and 19 June 1982, respectively. An experimental unit (subplot in K81 and subplot in K82) consisted of two rows, 4 m long, with 10 cm between plants in the row and 75 cm between rows. The exceptions were experimental units in BC_0 subplots, which consisted of four rows of which the center two were harvested.

Days to flower was recorded as the number of days from sowing to 50% anthesis in an experimental unit. The mean distance from the ground surface to the panicle tip for five competitive plants was recorded as plant height. Grain yield was the weight of all hand-harvested, sun-dried, threshed, and cleaned grain from an experimental unit. Kernel weight was the weight of a 100-kernel sample from an experimental unit.

Statistical analysis

The BC_2 was the only segregating generation evaluated in both K81 and K82. Adjusted population means were used when comparisons were made among backcross populations not evaluated in the same year. The adjusted population mean for a trait for the BC_g generation was calculated as

$$\overline{BC}_{agp} = \overline{BC}_{gp} \cdot (BC_{2\cdot} \div \overline{BC}_{2p})$$

where $\overline{BC}_{gp}$ is the mean of the BC_g generation of a given mating in year p and $\overline{BC}_{2\cdot}$ is the mean of the BC_2 of the mating over both years. Use of this formula assumes that the effects of years on population means were proportionally similar for all generations. Genetic variance components (s_g^2) within populations and experiments were computed using linear functions of appropriate mean squares and adjusted, as were means, for comparison across years.

Results

Parents

The three wild parents were taller and earlier than the cultivated parents and had very low yields and small kernels (Table 1).

Grain yields of two wild parents, virgatum and arundinaceum, may have been underestimated. Profuse and indeterminate tillering combined with a very short interval (within panicles) between physiological

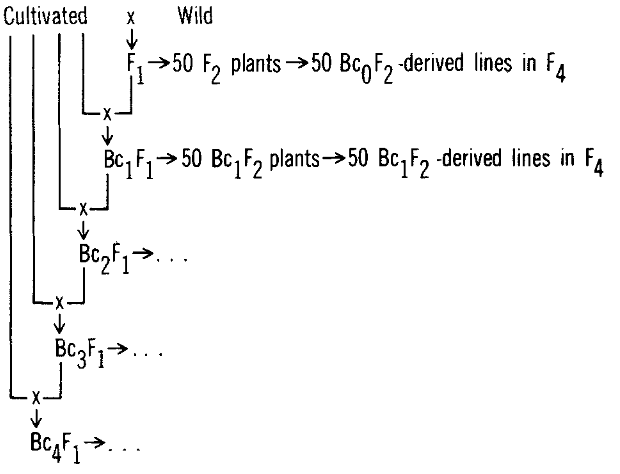

Fig. 1. Development of introgression populations

Table 1. Means over K81 and K82 of parents for five traits

Parent	Grain yield q/ha	100-kernel wt g	Days to flower da	Plant height cm	Threshing %
Cultivated					
'CK60B'	40.5	2.36	55.4	131	83.1
'RS/R/A2725'	45.6	2.07	60.2	210	80.9
SE	0.4	0.01	0.1	1	0.3
Wild					
'Virgatum'	1.3	0.50	46.0	221	21.0
'Arundinaceum'	6.1	0.50	55.0	289	57.5
'Verticilliflorum'	13.8	0.89	50.0	286	59.3
SE	2.1	0.07	0.5	5	1.5

maturity and onset of shattering resulted in loss of some seed before it could be harvested.

The 'verticilliflorum' parent probably contained some cultivated germplasm; it shattered less readily, tillered less profusely, and had larger kernels and higher grain yield. Nonetheless, all three wild parents were highly inferior in an agronomic sense. Wild parents were morphologically uniform and were treated as homozygous lines in the analysis.

Cultivated parent RS was higher-yielding, taller, and later than the dwarf CK60B.

Variation among matings

The effect of alleles from wild parents on yields were larger than those from cultivated parents (Tables 2 and 3); however, mating mean and wild parent per se yields were negatively correlated (Tables 1 and 3). There is no evidence of strong interactions between wild and cultivated parents (Table 2).

Variation among generation means

Unadjusted mean grain yields are given in Table 3. Variation among generations was significant within and across all matings for all traits (analyses of variance not shown). Standard errors of generation mean grain yields were 0.6 and 0.7 q/ha in K81 and K82, respectively.

The expected percentage of cultivated germplasm is 0, 50, 75, 87.5, 93.75, 96.875, and 100 for the wild parent, BC_0, BC_1, BC_2, BC_3, BC_4, and cultivated parent, respectively. Linear regression on average percentage cultivated germplasm accounted for 85.9 to 96.8% of the variation among seven generations (i.e., two parents plus the BC_0–BC_4) for grain yield in four matings, but the relationship was highly curvilinear in the two matings involving verticilliflorum, CK×SV and RS×SV (Table 4).

If the wild parents are excluded from the analyses, any deviations from linearity must be due to epistasis

Table 2. Analyses of variance among mating means within generations for grain yield

Source of variation	BC_0		BC_1		BC_2		BC_3		BC_4	
	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.	D.F.	M.S.
Replicates/experiments	1	35.9**	1	19.9	2	13.3*	1	2.1	1	13.2*
Experiments					1	1123.2**				
CP[a]	1	6.2	1	0.2	1	0.7	1	8.7	1	1.1
WP[b]	2	57.7**	2	71.2**	2	128.1**	2	10.8	2	8.0
CP × WP	2	5.7	2	4.9	2	56.6**	2	17.5	2	8.2
Experiments × CP					1	29.8**				
Experiments × WP					2	4.9				
Experiments × CP × WP					2	5.5				
Error	5	1.2	5	3.6	10	1.9	5	3.4	5	2.0

[a] Among means of progeny of cultivated parents
[b] Among means of progeny of wild parents
* Significant at the 5% level
** Significant at the 1% level

Table 3. Unadjusted means ($\bar{x}$) and genetic variances (s_g^2) for grain yield in q/ha for five backcross generations of six matings

Generation	CK × VI		CK × AR		CK × SV		RS × VI		RS × AR		RS × SV	
	$\bar{x}$	s_g^2	$\bar{x}$	s_g^2	$\bar{x}$	s_g^2	$\bar{x}$	s_g^2	$\bar{x}$	s_g^2	$\bar{x}$	s_g^2
							K81					
BC_0	16.1	13.4	12.9	28.4	11.5	17.9	17.3	13.2	12.1	14.2	7.4	31.6
BC_1	21.6	27.2	18.1	47.8	14.1	56.5	21.1	52.0	20.1	61.0	12.5	50.6
BC_2	28.3	8.2	25.3	26.8	23.2	43.4	31.9	66.1	20.2	74.7	19.1	36.8
							K82					
BC_2	37.5	38.3	37.4	57.9	33.7	108.2	43.8	30.7	33.3	84.9	36.3	68.4
BC_3	42.5	22.7	40.6	5.1[a]	42.4	50.3	45.3	9.8[a]	40.0	49.1	43.0	38.4
BC_4	45.4	33.8	46.2	4.3[a]	42.6	104.3	44.8	32.9	42.5	34.9	42.2	2.7[a]
Mean[b]	31.3		29.3		26.8		33.3		27.9		25.6	

[a] Mean square not significant
[b] Giving equal weight to all generations

Table 4. Percentage of variation among adjusted generation mean grain yields accounted for by regression on percent cultivated germplasm

Source of variation	Mating					
	CK×VI	CK×AR	CK×SV	RS×VI	RS×AR	RS×SV
All generations						
Linear	96.8**	92.1**	68.1**	96.1**	85.9*	60.4*
Quadratic	1.6	6.6*	28.1**	1.3	5.8	33.2*
Residual	1.6	2.3	3.8	2.6	8.3	6.4
Excluding wild parent						
Linear	92.8**	94.4**	87.8**	90.4**	79.6*	85.5**
Quadratic	7.2*	4.4*	10.3*	5.1*	5.9	8.6
Residual	0.0	1.2	1.9	4.5	14.5	5.8

*, ** Associated mean square significant at 5% and 1% level, respectively

(Cox 1984). Excluding the wild parent substantially increased the percentage of variation due to the linear model in verticilliflorum matings.

The curvilinear trend in verticilliflorum matings was strong; the BC_0 mean yield was similar to that of the wild parent mean in verticilliflorum matings (Fig. 2). Because BCF_2-derived lines in the F_4 were evaluated, heterozygosity was 12.5% or less; therefore, dominance cannot explain such extreme nonlinearity, even when the wild parent is excluded. The relationship was more nearly linear in virgatum and arundinaceum matings (Fig. 2), though the curve for arundinaceum matings was also slightly concave-upward (significantly so in CK×AR – Table 4).

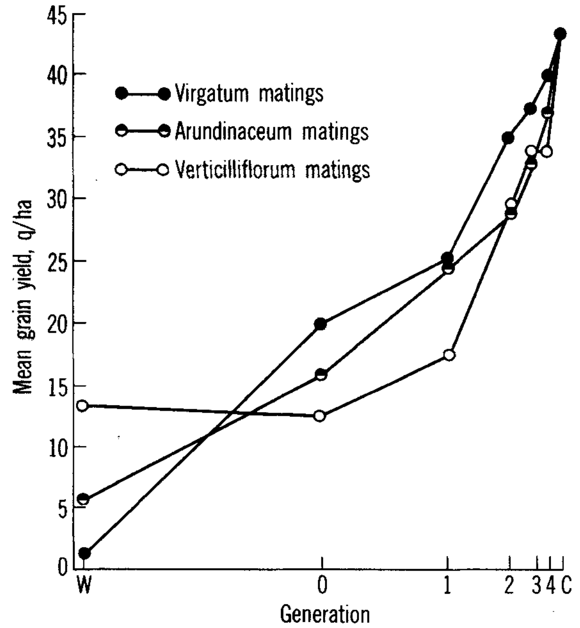

Fig. 2. Generation means for grain yield averaged over cultivated parents (*W* = Wild parent, *0* ... *4* = BC_0 ... BC_4, *C* = cultivated parent). Positions of generations on x-axis represent proportions of cultivated germplasm

Over all matings, kernel weight closely followed a linear trend, whereas a linear model accounted for only 38.7 and 42.9% of the variation (less than that due to residual variation) in days to flower and height, respectively (Table 5). Excluding the wild parent increased the linear component only for height.

Deviation from linearity for days to flower and height is illustrated in Fig. 3. The BC_0F_2 and all backcross generations were essentially equal to the recurrent parent for days to flower. Mean height of the BC_0 was greater than or similar to that of the wild parent in all matings, accounting for much of the curvilinearity for that trait.

In summary, mean progeny phenotype, especially in the BC_0, was closer to the wild parent phenotype than expected for yield in verticilliflorum and arundinaceum matings and for height in all matings. Mean kernel

Table 5. Percentage of variation among generation means for four traits accounted for by regression on percent cultivated germplasm (from a pooled analysis of all matings)

Source of variation	Trait			
	Grain yield	100-kernel wt	Days to flower	Plant height
All generations				
Linear	81.7**	92.8**	38.7	42.9
Quadratic	8.3	0.2	8.8	12.7
Residual	10.0	7.0	52.5	44.4
Excluding wild parent				
Linear	81.8*	81.6	0.0	61.7
Quadratic	6.4	3.8	0.0	0.0
Residual	11.8	14.7	100.0	38.3

*, ** Associated mean square significant at 5% and 1% level, respectively

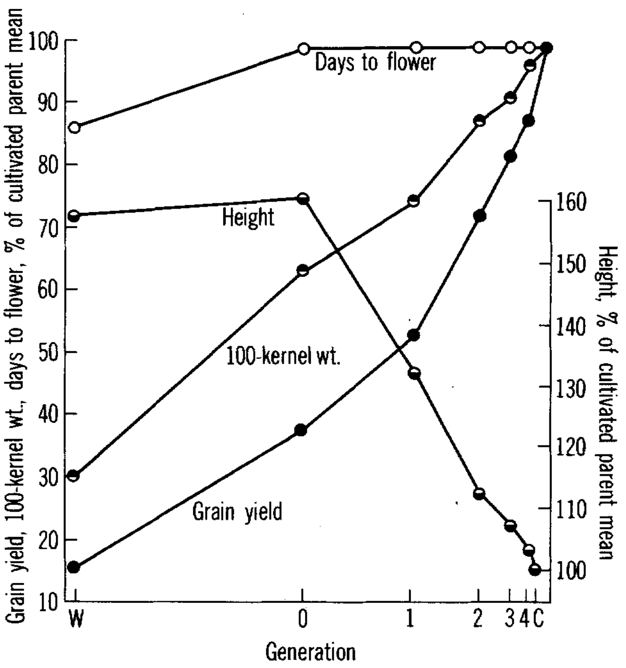

Fig. 3. Generation means (expressed as percent of cultivated parent mean) for days to flower, height, 100-kernel weight, and grain yield over all matings (*W* = wild parent, *0*... *4* = F_2, *C* = cultivated parent)

weight was closely related to percentage cultivated germplasm, and generations differed little for days to flower.

Variation within generations

There was significant genetic variation within most populations (i.e., generations in matings) for all traits (analyses of variance not shown).

Genetic variance components (s_g^2) for grain yield increased sharply from BC_0 to BC_1 in all matings (Table 3 and Fig. 4). In two matings, RS × VI and RS × AR, adjusted genetic variance for grain yield reached a maximum in the BC_2. The ratio $s_g^2(BC_2)/s_g^2(BC_0)$ was approximately 5.0 in these two matings, compared with an expected ratio of 0.61 (Cox 1984).

The increase in s_g^2 from BC_3 to BC_4 in CK × SV (Fig. 4) probably was due to sampling of a disproportionately large amount of wild germplasm in producing the BC_4F_2 because a similar increase occurred for all traits. There also was an increase in RS × VI from BC_3 to BC_4, but only for grain yield.

On the average, s_g^2 for grain yield declined from BC_1 to BC_4 as expected (Cox 1984), but the increase in s_g^2 from BC_0 to BC_1 differed strikingly from the expected patterns (Fig. 4). In cannot be determined from these data whether the curves in Fig. 4 resulted from depression of genetic variation in the BC_0, elevation of variance in the BC_1–BC_4, or both.

The change in s_g^2 for kernel weight over backcross generations was similar to that for grain yield (Fig. 5). For both traits, s_g^2 in the BC_1, averaged over matings, was over twice as large as s_g^2 in the BC_0. On the average, s_g^2 for days to flower and height followed expectations much more closely (Fig. 5), though large increases from BC_0 to BC_1 occurred for days to flower in verticilliflorum matings and for height in virgatum matings.

We obtained the expected coefficients of genetic variance for each backcross generation of each mating by substituting the numbers of F_1 families and F_2-derived lines evaluated per generation into formulas (15) of Cox (1984) and ignoring dominance variance. The coefficients were similar for all matings, and average values were 0.48, 0.48, 0.29, 0.15, and 0.07 for the BC_0, BC_1, BC_2, BC_3, and BC_4, respectively.

Predicted genetic variances ($\hat{s}_g^2$) for all populations were obtained by a least-squares fit of observed s_g^2 values to the coefficients. A chi-square statistic was obtained for each mating and trait using the formula

$$\chi^2 = \sum_{BC_0}^{BC_4} \frac{(s_g^2 - \hat{s}_g^2)^2}{V(s_g^2)}$$

where $V(s_g^2)$ is the variance of s_g^2, computed from variances of unadjusted genetic variance components (not shown).

Chi-square values were highly significant in all cases except height in CK × AR, days to flower in RS × AR, and grain yield in RS × SV (Table 6), confirming what is visually obvious in Figs. 4 and 5.

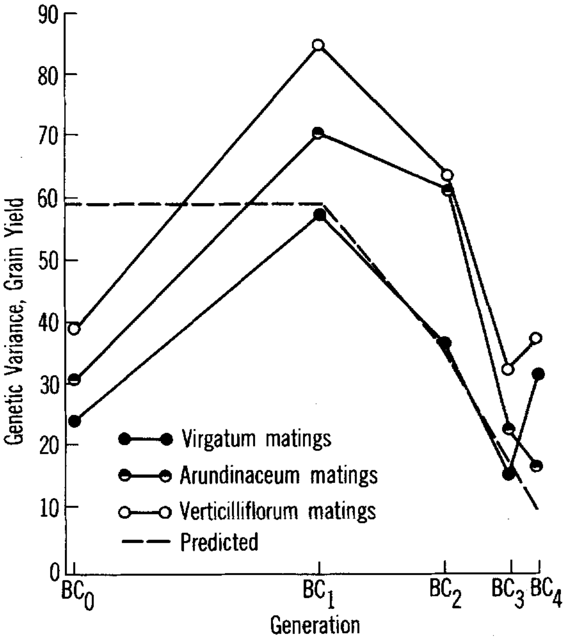

Fig. 4. Adjusted generation genetic variances for grain yield, averaged over wild parents, and the mean predicted genetic variances based on least-squares fits to coefficients

Table 6. Chi-square values for the fit of genetic variances in the BC_0 to BC_4 to variances predicted by a simple additive model (with probability of a greater value in parentheses)

Mating	Trait			
	GY	KW	FL	HT
CK×VI	8.21 ($0.05<P<0.10$)	14.56 ($0.001<P<0.01$)	116.6 ($P<0.001$)	8.37 ($0.05<P<0.10$)
CK×AR	8.65 ($0.05<P<0.10$)	13.48 ($0.001<P<0.01$)	290.7 ($P<0.001$)	7.02 (ns)*
CK×SV	48.63 ($P<0.001$)	26.09 ($P<0.001$)	103.5 ($P<0.001$)	156.57 ($P<0.001$)
RS×VI	34.71 ($P<0.001$)	49.92 ($P<0.001$)	19.07 ($P<0.001$)	70.48 ($P<0.001$)
RS×AR	25.10 ($P<0.001$)	19.46 ($P<0.001$)	5.29 (ns)	13.29 ($0.001<P<0.01$)
RS×SV	6.50 (ns)	18.66 ($P<0.001$)	10.73 ($0.02<P<0.05$)	13.54 ($0.001<P<0.01$)

* $P<0.10$

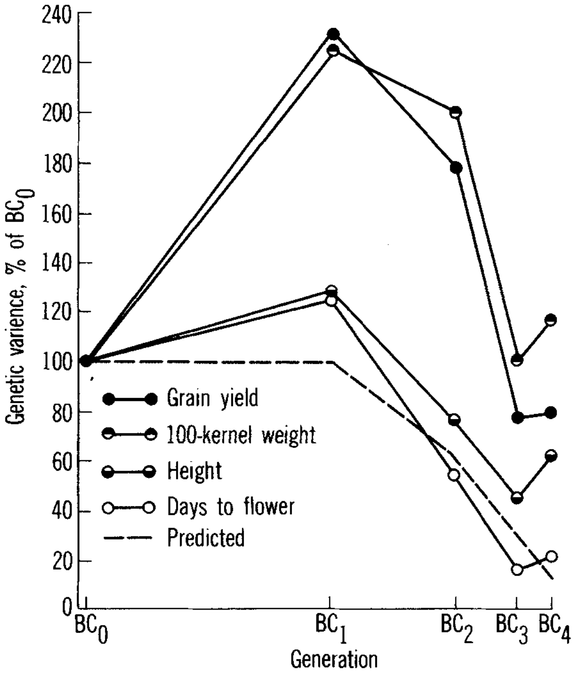

Fig. 5. Generation genetic variances for grain yield, 100-kernel weight, height, and days to flower, averaged over all matings, and the mean predicted genetic variances based on least-squares fits to coefficients

Discussion

Three unexpected and perhaps interrelated results were obtained for grain yield: (1) a negative correlation between the yield of wild parents and the mean of their progeny; (2) a curvilinear, concave-upward, relationship between generation means and percentage cultivated germplasm (especially in verticilliflorum matings); and (3) an increase in genetic variance after one or two backcrosses.

The first two results suggest that genes in verticilliflorum, and possibly arundinaceum, "mask" the effects of genes from the cultivated parents. This tends to hold grain yield at a low level in these matings relative to their parents and to virgatum progeny, causing the three curves in Fig. 2 to intersect between 0 and 50% cultivated germplasm (i.e., between wild parent and BC_0).

The third result agrees with the common observation (DeWet et al. 1970) that in natural wild × cultivated sorghum crosses, genetic variation is very limited in the BC_0 but that backcrossing "releases a tremendous amount of variability". This phenomenon might also be due to "masking" genes as illustrated by the following example.

If wild sorghum contains regulatory elements that suppress effects of alleles at other loci controlling grain yield, one backcross could reduce the frequency of the wild regulatory "alleles" from 0.5 to 0.25 in random lines. With completely additive gene action, $s_g^2(BC_0) \simeq s_g^2(BC_1)$ (Cox 1984), and the presence of regulatory alleles could make $s_g^2(BC_0) < s_g^2(BC_1)$.

For example, consider a two-locus genetic model (with no linkage), in which a dominant regulatory allele B from the wild parent suppresses variation at another locus that has alleles A and a, as in Model 1 of Table 7 and in Fig. 6. The strength of regulation can vary from $e=1$ (no effect of B) to $e=-1$ (no variation due to locus A in the presence of B), but there is no dominance at locus A for any value of e.

In this situation, $s_g^2(BC_1) > s_g^2(BC_0)$, and the difference increases as e approaches -1 (Fig. 7). If

Table 7. Values and frequencies of BC_gF_2 plants for two-locus epistatic models

Genotype	Genotypic value		Frequency (×256)		
	Model 1	Model 2	BC_0	BC_1	BC_2
aa BB (wild)	$-x$	ex	16	4	1
aa Bb	$-x$	ex	32	8	2
aa bb	$-x$	x	16	20	13
Aa BB	$\frac{1}{2}(e-1)x$	0	32	8	2
Aa Bb	$\frac{1}{2}(e-1)x$	0	64	16	4
Aa bb	0	0	32	40	26
AA BB	ex	$-ex$	16	20	13
AA Bb	ex	$-ex$	32	40	26
AA bb (cult.)	x	$-x$	16	100	169
Model 1 mean			$\frac{1}{8}(-3+3e)x$	$\frac{1}{32}(7+9e)x$	$\frac{1}{128}(75+21e)x$
Model 2 mean			0	$\frac{1}{32}(-10-3e)x$	$\frac{1}{64}(39-9e)x$

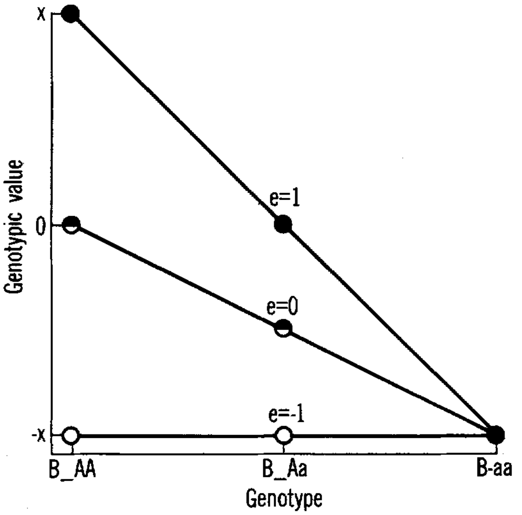

Fig. 6. A graphical representation of genotypic values for B genotypes when *e = 1, 0,* and *– 1* in Table 7, Model 1

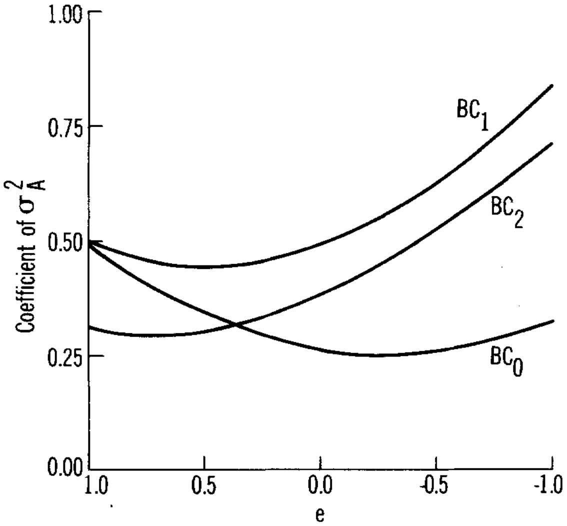

Fig. 7. Plot of genetic variance versus e for Model 1 in three backcross generations

$e < 0.375$, $s_g^2(BC_2) > s_g^2 BC_0$). Note that for most values of e, $s_g^2(BC_0)$ is depressed and $s_g^2(BC_1)$ elevated, compared with their values for $e = 1$ (no regulation).

For $e < 1$ in Model 1, two-locus means of backcross generations are closer to that of the wild parent than when $e = 1$ (Table 7). The magnitude of effect on means summed over loci depends on the distribution of plus and minus alleles between the parents, i.e., the signs of the x's for each of the loci. In this study, significant depression of backcross means relative to the midparent occurred for grain yield in verticilliflorum and arundinaceum matings.

Model 1 is less likely to explain the increase in genetic variances in virgatum matings, since means increased linearly. Virgatum matings, however, produced a considerable number of high-yielding lines, suggesting that there are "wild" genes for high grain yield that are not expressed in virgatum itself. One could postulate "B" alleles that may not only suppress variation but also reverse the effects of plus genes from the wild parent, as in Table 7, Model 2. When $e = -1$, both parental means are $-x$ and means of segregating generations are greater than when $e = 1$. BC_1 and BC_2 genetic variances (not shown) are 150 and 131%, respectively, of the BC_0 genetic variance. Model 2 systems operating in addition to Model 1 systems could produce the trends in means and genetic variances observed in virgatum matings.

Britten and Davidson (1969, 1971) described a model for gene regulation in which a series of integrator genes controls the output of producer genes through networks of varying complexity. Loci behaving as do B and A above can be incorporated in such a network as integrator and producer loci, respectively, with the end phenotype being a quantitative trait such as grain yield.

In this system, backcrossing can increase genetic variance. Producer alleles with positive effects on phenotype can come from either or both parents. The size of the increase in variance depends on the relationships of integrator and producer loci and strength of regulation (value of "e").

Any kind of interlocus interaction is exceedingly difficult to detect experimentally (Barker 1979) and the data from this study certainly do not prove that epistasis was present. However, the following alternative explanations of these results are inadequate: *(1) The cultivated parent contributes mostly recessive alleles.* Intralocus interaction can cause up to 12% increase in genetic variance from BC_0 to BC_1 when BCF_2-derived lines in the F_4 are evaluated (Cox 1984), but even this increase requires all "cultivated" alleles to be completely recessive and positive in effect. (Increases in this study ranged from 60 to 328%); *(2) Repulsion linkages are broken in the first backcross, increasing additive genetic variation.* The extent of additional recombination at meiosis in the BC_1F_1 is sufficient to cause only a small increase in variance (Cox 1984); *(3) The genetic variance of the BC_1 is inflated by genotype-environment interaction to a greater extent than is that of the BC_0.* Line × year interaction for yield in this study was significant for BC_2 lines in only two matings. Genetic variance of yield, in other experiments (Cox 1983) involving these same matings evaluated over two seasons (rainy and dry), and thus free of the line × season component, averaged 236 and 164% in the BC_1 and BC_2, respectively, relative to the BC_0; *(4) The results are due to the large standard errors of variance components.* Standard errors of variance components for grain yield in the BC_0 and BC_1 ranged from about 8 to 16 for the six matings; the difference $s_g^2(BC_1) - s_g^2(BC_0)$ ranged from 27 to 67. The increase occurred in all matings for grain yield and in five of six matings for kernel weight. Similar, though smaller, increases in genetic variance were found also in introgression studies involving oats (Lawrence and Frey 1976) and barley (Rodgers 1982); *(5) Genetic variances increased because means increased.* If increased genetic variance is due to an inflated scale of measurement in the BC_1, compared with BC_0, error variances would be expected to increase similarly. Error variances increased an average of only 28% from BC_0 to BC_1, compared with 132% for genetic variances.

The change in s_g^2 with backcrossing in cases of complete dominance, repulsion linkage, and Model 1-type regulation (e = − 1) is illustrated in Fig. 8.

It is quite plausible that there are strong regulatory elements in wild sorghums that are lacking in cultivars. Hedrick and McDonald (1980) showed that in times of drastic changes in selection pressure, the most rapid adaptation would occur via changes in frequencies of regulatory alleles. Domestication of a wild species is a very drastic change in selection pressure, and null alleles at regulatory loci that affect agronomic traits might be among the first fixed during domestication.

Genetic variance for kernel weight followed a pattern similar to that for grain yield, but means increased linearly. Genetic variance and means for days to flower and plant height deviated significantly from expectations, but only for mean plant height was the deviation extreme. These results taken together indicate some degree of epistasis, especially for height, despite the relatively simple inheritance of major height differences within the cultivated subspecies (Quinby 1974).

If the postulated regulatory mechanisms are important in wild × cultivated sorghum crosses, plant breeders utilizing such crosses must (1) evaluate progeny rather than wild accessions per se when choosing parents inasmuch as useful wild genes may be suppressed, (2) backcross at least once to lower the frequency of "wild" regulatory alleles, and (3) evaluate large populations because the frequency of agronomically superior lines may be reduced.

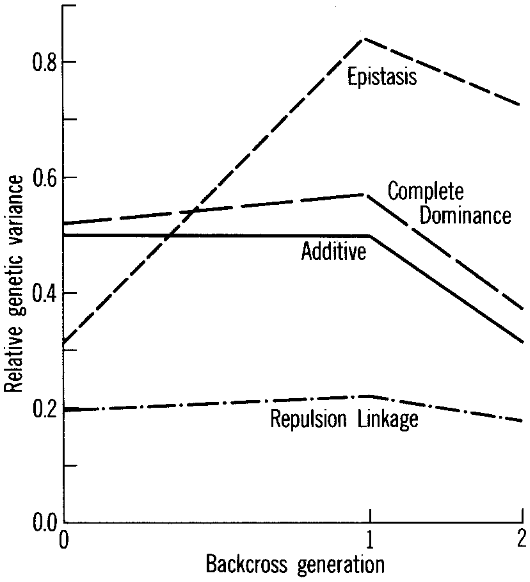

Fig. 8. Change in genetic variance with backcrossing for two-locus epistasis with Model 1, e = − 1 (– – –), all plus alleles recessive and in cultivated parent (—— —), no dominance, epistasis or linkage (——), and two-locus repulsion linkage with recombination frequency of 0.2 (– · –) for F_2-derived lines in F_4. The last three curves are from formulas in Cox (1984)

Finally, for improvement of introgression populations, recurrent selection is necessary to eliminate undesirable "wild" regulatory alleles (if present) and increase the frequency of desirable "wild" producer alleles, which will be low in later backcrosses.

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