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Estimates of Quantitative Genetic Parameters in IAP2B(M) Random-Mating Sorghum Population[1]

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Random-mating populations of sorghum [*Sorghum bicolor* (L.) Moench] are used extensively as germplasm in the development of parental lines for hybrids. Populations improved by recurrent selection provide a useful source for the selection of superior parental lines. Our objective was to determine the effectiveness of mass selection for threshed-panicle weight by comparing the performance of lines (S_1 families) chosen randomly from C0 and C4 of sorghum population IAP2B. Sixty S_1 families from each cycle were grown in five Iowa environments.

Four cycles of selection for panicle weight shifted the mean for grain yield favorably, and the range among families was extended. Increased values in C4 also were observed for seeds/panicle, 100-seed weight, days to midbloom, and plant height, but panicles/plant decreased. Genotypic variance among S_1 familes increased from C0 to C4 for grain yield and days to midbloom. Heritability estimates for grain yield also increased from C0 to C4. Expected gain/year for grain yield by using S_1 family selection increased from 2.0% of the mean for C0 data to 3.2% for C4.

Correlation coefficients indicated that selection for individual-panicle grain weight also influenced other characters. Correlations changed substantially in a positive direction from C0 to C4 for grain yield vs. seeds/panicle and grain yield vs. panicles/plant, but they changed in a negative manner for grain yield vs. 100-seed weight. IAP2B(M) should prove useful for developing female parents with a wide array of gene combinations. Higher estimates of genotypic variance and heritability for grain yield in C4 compared to C0, as well as greater expected gain in C4 from S_1 family selection, indicated that further improvement of the population should be expected with additional cycles of selection.

INDEX DESCRIPTORS: *Sorghum bicolor* L. Moench, agronomic traits, breeding systems, mass selection.

Recurrent selection has been used in numerous plant species to increase the frequency of favorable alleles for both qualitatively and quantitatively inherited characters. When additive gene action plays a major role in the heredity of a trait, improvement of populations *per se* also should improve the performance and general combining ability of inbred lines developed from those populations.

The incorporation of genetic male sterility into sorghum [*Sorghum bicolor* (L.). Moench] germplasm has provided a means for making large-scale cross pollinations. With the use of genetic male sterility, numerous random-mating populations have been formed and many have been characterized for quantitative genetic parameters (Doggett, 1988). Additive genetic variance is a large component of the total genetic variance for most traits. Phenotypic recurrent selection has been used to take advantage of additive genetic variance, and numerous improvements in sorghum random-mating populations have been reported (Ross and Gardner, 1983).

Mass selection of individual plants has been used effectively in sorghum for characters that are highly heritable (Doggett, 1968). It is a low-cost method of population improvement that provides a useful alternative when funds and staff are limited (Doggett, 1968; Ross et al., 1971; Lothrop et al., 1985a; Kwolek et al., 1986; Ess and Atkins, 1989; Secrist, 1989). Selection can be based on the phenotype of the individual organism without consideration of the performance of its progeny.

The objectives of our research with sorghum population IAP2B (Atkins, 1982) were (i) to evaluate the breeding potential of the population *per se*, and (ii) to determine the effectiveness of mass selection for threshed-panicle weight by comparing lines (S_1 families) chosen randomly from initial (C0) and fourth cycle (C4) isolation plantings.

MATERIALS AND METHODS

The development of IAP2B(M) was initiated by making controlled pollinations of 10 nonrestorer lines (B-lines to the milo A1 cytoplasm system) onto bagged genetic male-sterile (ms_3) panicles of NP2B population (Nordquist et al., 1973). NP2B was constituted from intermated seed of backcrosses of eight B-lines to A1 cytoplasm ('Combine Kafir-60', 'Martin', 'Reliance', 'Westland', 'Wheatland', 'Redlan', 'Dwarf Redlan', and Tx606) that carried Coes ms_3. The 10 B-lines (to A1 cytoplasm) used in developing IAP2B(M) were 'Redbine-58', WD4, OKY54, OKY55, KS12, KS18, KS22, KS24, KS56, and KS57. The component parental lines for both populations are adapted for production in the midwestern United States.

Equal weights of seed for the 10 crosses were composited, and approximately 6,000 plants were grown in isolation near Ames, IA, in 1978 and in each succeeding year through 1982. Gridded mass selection was practiced each year (cycle), with 500 to 600 tagged male-sterile panicles harvested annually. Very late or tall plants were not selected. Equal amounts of seed of the 10 largest panicles (seed weight) from each of 30 cells within the grid were composited to advance each cycle of selection.

Our experiment evaluated the performance of 120 S_1 familes, 60 chosen randomly from C0 and C4. Tests were conducted at the Iowa State University Agronomy Research Center near Ames, IA in years 1984 through 1988. The soil type was Nicollet (fine-loamy, mixed, mesic Aquic Hapludolls). All plantings were made between 21 May and 4 June, using a replications-within-sets field design. There were six sets in each year, two replicates per set, with 10 S_1 families from C0 and 10 from C4 assigned randomly within each replication. Individual plots were single rows 4.27 m long with 1.02 m between rows. Seedlings in the row were thinned to about 10 cm apart (97,000 plants/ha).

Data were obtained from a 3.05-m section of each plot for plants/plot, panicles/plot, and weight of dry unthreshed panicles; g/100 seed was determined from a threshed sample of three panicles/plot. Grain yield was estimated by using the procedure described by Robinson and Bernat (1963). Additional characters calculated from these data were panicles/plant and seeds/panicle. Data also were recorded for days to midbloom (planting to 50% anthesis) and plant height.

All effects were considered random in the combined analyses of variance. Genotypes (S_1 families) and environments (years) were considered random for estimation of the variance components σ^2 (error variance), σ^2_{ge} (genotype-environment interaction variance), and σ^2_g

Table 1. Means, standard errors and high and low S_1 family values for agronomic traits measured at Ames, Iowa during 1984-88.

Trait and cycle of selection	Mean	Low S_1 family value	High S_1 family value	F test† CO mean vs. C4 mean
Grain yield (Mg/ha)				
C0	5.41±0.017	4.51	6.08	**
C4	5.66±0.018	4.89	6.66	
Seeds/panicle				
C0	1634±10	1239	1967	**
C4	1679±9	1244	2094	
100-seed weight (g)				
C0	2.45±0.011	1.99	3.10	**
C4	2.54±0.009	1.93	3.20	
Panicles/plant				
C0	1.53±0.007	1.26	1.94	**
C4	1.51±0.007	1.20	1.90	
Days to midbloom‡				
C0	67.1±0.32	63.2	70.2	**
C4	68.7±0.36	64.5	72.5	
Plant height (cm)‡				
C0	113±0.056	97	139	**
C4	122±0.058	103	148	

†, **Differences significant beyond P<0.01.
‡Measurements made during 1986-88.

(genetic variance). Approximate confidence intervals $(1 - \alpha = 0.90)$ for the variance components were calculated by using procedures described by Knapp et al. (1987).

Heritabilities (h^2) on an entry-mean basis were calculated as the ratio of genotypic variance (σ_g^2) to phenotypic variance (σ_{ph}^2) by using the formula presented by Hallauer and Miranda (1988, p. 90-91). Exact confidence intervals $(1 - \alpha = 0.90)$ for the heritability estimates were calculated by using the procedures explained by Knapp et al. (1985, 1987)

Estimated response to selection (ΔG) by recombining selected families was calculated by using the formula presented by Falconer (1981, p. 175). Correlated response among characters to selection (CR_{yx}) also was determined by using the formula of Falconer (1981, p. 283). Phenotypic correlations (r_{ph}) among characters were calculated by using established procedures. Genotypic correlations (r_g) were derived by using the formula:

$$r_g = \frac{\sigma g(xy)}{\sqrt{\sigma^2 g(x)} \ \sqrt{\sigma^2 g(y)}}$$

where $\sigma g(xy)$ = the genotypic covariance between traits x and y, $\sigma_g^2(x)$ = the genotypic variance for trait x, and $\sigma^2 g(y)$ = the genotypic variance for trait y.

RESULTS

Environmental conditions in Iowa during 1984 through 1988 generally were favorable for growth and development of sorghum. The experiments in 1984, 1986, and 1988 were most productive, with an average grain yield of 6.07 Mg ha^{-1}. High summer temperatures in 1987 resulted in early maturation of plants and a mean yield of 5.00 Mg ha^{-1}. Rainfall was sparse throughout the summer in 1985, resulting in a mean yield of 4.45 Mg ha^{-1}.

Four cycles of selection for threshed-panicle weight resulted in significant (P<0.05) increases in the means for grain yield, seeds/panicle, 100-seed weight, days to midbloom, and plant height, but panicles/plant were significantly fewer (Table 1). The ranges among S_1

family means also increased from C0 to C4 for all characters. Estimates of genotypic variance, with approximate confidence intervals (Table 2), indicated that genetic variability among S_1 families increased significantly from C0 to C4 for grain yield and days to midbloom. Differences for variance component estimates between C0 and C4 for the other characters did not surpass limits established by the confidence intervals.

Heritability estimates with exact confidence intervals also are shown in Table 2. Values for h^2 increased significantly for grain yield from C0 to C4 (from 0.68 to 0.78), but they decreased significantly for panicles/plant (from 0.85 to 0.74). Heritability for the other characters differed between C0 and C4, but not beyond the established confidence intervals.

Expected responses from S_1-family selection that uses replicated yield trials and the gains that were realized by using gridded mass selection for threshed panicle weight are presented in Table 3. The expected gains were derived by using variance-component and heritability estimates from Table 2 along with a 10% selection intensity. Expected gain/year for grain yield achieved by using S_1 family selection increased from C0 to C4 (from 2.0% to 3.2% of the mean), but decreased for panicles/plant (from 4.5% to 3.6% of the mean). Differences between C0 and C4 for expected gains were considerably smaller for the other traits.

Empirical values listed in Table 3 for gains determined after four cycles of gridded mass selection for individual-panicle grain yield provide a comparison between gains predicted for S_1 testing and actual gains realized from mass selection in IAP2B. Gains observed from mass selection were considerably smaller for all traits than the gains estimated for S_1-family selection. A factor that contributed to the lower realized gain in yield from mass selection relative to that predicted for S_1 selection was the lower selection intensity in the former. The selected proportion for mass selection was about 50%, and this was indirect selection based on panicle weight. Therefore, the modest gain obtained relative to direct S_1 selection at 10% intensity is not due entirely to heritability in plant versus family selection.

Table 2. Genotypic variance components with approximate confidence intervals and heritability, on the basis of entry-means, with exact confidence intervals for agronomic traits measured at Ames, Iowa during 1984-88.

Trait and cycle of selection	Genotypic variance	Confidence intervals		Heritability	Confidence intervals	
		Lower limit	Upper limit		Lower limit	Upper limit
Grain yield (Mg/ha)						
C0	0.054†	0.033	0.088	0.68†	0.55	0.78
C4	0.123	0.083	0.189	0.78	0.70	0.85
Seeds/panicle						
C0	24981	17262	37678	0.82	0.75	0.88
C4	26554	17900	40458	0.79	0.71	0.86
100-seed weight (g)						
C0	0.047	0.033	0.070	0.85	0.79	0.90
C4	0.047	0.033	0.070	0.86	0.80	0.90
Panicles/plant						
C0	0.017	0.012	0.025	0.85†	0.79	0.90
C4	0.012	0.008	0.018	0.74	0.63	0.82
Days to midbloom‡						
C0	2.28†	1.59	3.41	0.84	0.77	0.89
C4	3.83	2.74	5.64	0.89	0.84	0.93
Plant height (cm)‡						
C0	79.0	57.0	115.2	0.91	0.87	0.94
C4	102.6	74.0	149.8	0.91	0.87	0.94

†Estimates of genotypic variance and heritability of C0 and C4 were significantly different in accordance with confidence intervals $(1 - \alpha = 0.90)$.
‡Measurements made during 1986-1988.

Table 3. Expected gain from S_1-family selection for grain yield and realized gain for agronomic traits after four cycles of gridded mass selection for individual-panicle grain weight, measured at Ames, Iowa, during 1984-1988.

Trait and cycle of selection	Expected from S_1 family selection (with 3 yr/cycle)		Realized from gridded mass selection (with 1 yr/cycle)	
	Gain/ year	Gain/year (% of mean)	Gain/ year	Gain/year (% of mean)
Grain yield (Mg/ha)				
C0	0.11	2.0		
C4	0.18	3.2	0.06	1.2
Seeds/panicle				
C0	83.6	5.1		
C4	84.3	5.0	11.3	0.7
100-seed weight (g)				
C0	0.116	4.7		
C4	0.117	4.6	0.023	0.9
Panicles/plant				
C0	0.069	4.5		
C4	0.054	3.6	−0.005	−0.3
Days to midbloom†				
C0	0.81	1.2		
C4	1.08	1.6	0.4	0.6
Plant height (cm)†				
C0				
	4.9	4.3		
C4	5.6	4.6	2.25	2.0

†Measurements made during 1986-1988.

Coefficients of correlation (Table 4) changed substantially in a positive direction from C0 to C4 for grain yield vs. seeds/panicle and grain yield vs. panicles/plant, but they changed in a negative manner for grain yield vs. 100-seed weight. The positive correlations between grain yield and days to midbloom, 100-seed weight and plant height, and panicles/plant with plant height were similar in C0 and C4, as were the negative correlations between seeds/panicle and 100-seed weight and seeds/panicle with plant height. Phenotypic and genotypic coefficients of correlation among characters usually were similar in magnitude.

Estimates of correlated response among characters determined from C0 data (Table 5) indicated that S_1 family selection for grain yield (i.e., threshed-panicle weight) would be expected to reflect a moderate increase in days to midbloom and small increases in seeds/panicle, 100-seed weight, panicles/plant, and plant height. The C4 data indicated that responses of seeds/panicle and panicles/plant to selection for grain yield would be much greater than predicted, but the response for 100-seed weight was estimated to be less. Indirect selection for grain yield by selecting for a yield component, days to midbloom, or plant height, lacks strong support from the estimates listed in Table 5. Moderate gains would be expected for grain yield, on the basis of both the C0 and C4 results, if selection were for days to midbloom.

DISCUSSION

A favorable shift in mean performance for the character under selection is a primary goal of recurrent selection. Mean grain yield of the individual S_1 families increased significantly from C0 to C4 (Table 1). Compared to yield of the base population, grain yield increased 1.15% per cycle over four cycles of selection. Regression analyses of data from supplementary experiments with C0 through C4 composites of S_1 and half-sib families did not indicate a significant linear, quadratic, or cubic regression in association with the increased grain yield over cycles (Maves, 1989).

Recurrent selection for one trait may result in changes in other traits. In our research, four cycles of selection for threshed-panicle weight significantly (P<0.01) increased the means for seeds/panicles, 100-seed weight, days to midbloom, and plant height, but decreased mean panicles/plant. Although differences between C0 and C4 exceeded the 0.01 level of probability, they were not large. Progression of these trends over additional cycles, however, should lead to differences of greater consequence.

A second goal of the selection in IAP2B was to maintain genetic variability for the trait under selection. Genotypic variance among S_1 families for grain yield (Table 2) increased significantly from C0 to C4. The higher estimate of variance in C4 may reflect repulsion-phase linkage disequilibrium in the base population (C0). The population was constituted by compositing equal portions of seed from crosses of 10 inbreds onto male-sterile plants of an existing random-mating population (Atkins, 1982). Good inbreds from diverse backgrounds might be expected to have favorable alleles at different loci, resulting in repulsion-phase disequilibrium among crosses. The C0 population was not intermated further before the S_1 families were selected for our experiments. S_1 families were chosen randomly from that population and evaluated along with S_1 familes from C4.

Hanson (1959) suggested a minimum of four parents and three to four generations of intermating in the synthesis of a base population. By using that strategy, Hanson believed that a base population should approach linkage equilibrium. Without intermating, it seems unlikely that our base population was in linkage equilibrium. As selection progressed over cycles, selected parents were intermated and new genetic combinations evolved. The breaking of gene association with these intermatings could contribute substantially to the increased genotypic variance for grain yield. If the frequency of favorable alleles was low in the base population, subsequent increases in frequency of favorable alleles should augment the genotypic variance for grain yield in C4. Estimates of genotypic variance also increased from C0 to C4 for

Table 4. Phenotypic (above diagonal) and genotypic (below diagonal) coefficients of correlation among agronomic traits in C0 and C4 of IAP2B(M) at Ames, Iowa, during 1984-1988.

Trait and cycle of selection	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Days to midbloom	Plant height
Grain yield						
C0		0.12	0.25	0.17	0.44**	0.05
C4		0.49**	−0.13	0.38**	0.41**	0.07
Seeds/panicle						
C0	0.08		−0.56**	−0.56**	0.26	−0.54**
C4	0.53		−0.65**	−0.18	0.17	−0.46**
100-seed weight						
C0	0.28	−0.54		−0.17	−0.12	0.43**
C4	−0.15	−0.64		−0.30*	−0.11	0.34*
Panicles/plant						
C0	0.15	−0.61	−0.21		−0.03	0.38**
C4	0.43	−0.15	−0.37		0.15	0.38**
Days to midbloom†						
C0	0.55	0.26	−0.15	−0.05		−0.04
C4	0.50	0.20	−0.15	0.23		0.20
Plant height†						
C0	0.12	−0.63	0.52	0.48	−0.04	
C4	0.13	−0.53	0.37	0.51	0.20	

*,**Significant beyond the 0.05 and 0.01 probability levels, respectively.
†Measurements made during 1986-1988.

Table 5. Expected correlated response in other traits when S_1 family selection is for grain yield, seeds/panicle, 100-seed weight, panicles/plant, days to midbloom, or plant height, determined from measurements made at Ames, Iowa, during 1984-1988.[†]

Trait and cycle of selection	Grain yield	Seeds/ panicle	100- seed weight	Panicles/ plant	Days to midbloom	Plant height
Grain yield						
C0	100.0	6.2	20.5	10.8	40.1	8.5
C4	100.0	48.3	− 13.2	40.9	42.8	10.8
Seeds/panicle						
C0	−9.0	100.0	−51.0	− 57.7	24.8	− 57.2
C4	49.4	100.0	− 56.8	− 12.4	17.4	−45.8
100-seed weight						
C0	29.7	− 51.0	100.0	− 19.2	− 13.9	47.0
C4	− 15.2	− 64.1	100.0	− 37.0	− 14.2	34.8
Panicles/plant						
C0	16.0	− 59.8	− 19.9	100.0	− 4.5	44.4
C4	37.9	− 13.4	− 31.0	100.0	18.7	41.8
Days to midbloom[‡]						
C0	53.1	27.7	− 13.6	− 5.2	100.0	− 4.4
C4	55.4	20.2	− 15.4	27.8	100.0	20.4
Plant height[†]						
C0	12.3	− 69.4	49.8	55.6	− 4.1	100.0
C4	14.3	− 54.5	38.7	63.8	19.9	100.0

[†]Responses expressed as percentages of expected gain from direct S_1-family selection for a given character.
[‡]Measurements made during 1986-1988.

days to midbloom, but they did not change significantly for the other characters (Table 2).

Although a reduction from C0 to C4 was shown for heritability of panicles/plant, the estimates were similar to those reported from experiments with other random-mating sorghum populations (Lothrup et al., 1985a; Jan-orn et al., 1976; Eckebil et al., 1977). Heritability estimated for other traits among S_1 families of IAP2B changed very little from C0 to C4, and the estimates generally are in harmony with those reported by Jan-orn et al. (1976), Eckebil et al. (1977), Lothrup et al. (1985a), Kwolek et al. (1986), and Ess and Atkins (1989).

Our results indicated an expected gain with S_1-family selection for grain yield of 2.0% per year (or generation) based on C0 data, and 3.2% per year for C4 data. Lothrop et al. (1985b) estimated yield gains/generation of 4.6% and 4.2% from two experiments that involved yield testing of S_1 families from IAP1R population. They also estimated yield response from gridded mass selection, and obtained values of 1.9% and 0.6% per generation for the two experiments. The gain per year in grain yield realized with mass selection in our experiments was 1.2%. The logistics of mass selection are much less consuming of project resources than are replicated yield trials of S_1 families.

Selection for individual-panicle grain weight in IAP2B has influenced associations of other characters with yield (Table 4). Of special importance, grain yield displayed little correlation with seeds/panicle in C0, but in C4 moderately strong correlation ($r_g = 0.53$, $r_{ph} = 0.49$) existed between these traits. Investigations with other random-mating sorghum populations have shown that seeds/panicle and seeds/plant usually were the components most highly correlated with grain yield (Ess and Atkins, 1989; Jan-orn et al., 1976; Lothrop et al., 1985b).

Indirect selection for grain yield should be successful if a component of yield is more highly heritable than yield and there is a substantial positive correlation between the two traits. Most genotypic correlations among agronomic traits for IAP2B were not strong enough to facilitate effective use of indirect selection. Improvement of grain yield

by selecting late-maturing genotypes seems to offer the greatest potential for effective indirect selection in this population (Tables 4 and 5). But the increased yield might be at the cost of adaptation or greater risk of frost damage.

It is noteworthy as well that selection of S_1 families for seeds/ panicle, based on the C4 data, would be expected to produce an improvement in grain yield that would be nearly half the increase expected with direct selection for yield. Based on the C0 data, however, selection for seeds/panicle would have resulted in an expected loss of 9% for grain yield. If the trend toward a greater correlation between grain yield and seeds/panicle should persist through subsequent cycles, selection of S_1 families with many seeds/panicle could be an effective strategy for increasing grain yield. It is operationally simpler, however, to select on a family basis for grain yield per se than it is to select for seeds/panicle or other components of yield. And all correlated responses to selection for yield were favorable except for the small reduction in seed size predicted from the C4 data.

Genetic and agronomic parameters determined for the C0 and C4 genotypes indicated that IAP2B(M) sorghum population should provide germplasm useful for developing female parents that possess a wide array of genes and gene combinations that are needed to diversify hybrid sorghum seed production. The higher estimates of genotypic variance and heritability for grain yield in C4, as well as larger estimates of expected gains from S_1-family selection, indicate that further improvement of the population should be expected with additional cycles of recurrent selection.

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