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Comparison of Mass Selection and S₁ Testing Recurrent-Selection Methods in Sorghum¹

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Mass selection and S_1 testing are often used for the improvement of sorghum *[Sorghum bicolor* (L.) Moench] populations. Both recurrentselection methods have a place in applied breeding programs and should be used where they are likely to be most advantageous. S_1 families of a random-mating sorghum population mass selected three cycles (C3) for individual-panicle weight [IAP1R(M)C3] were compared with S_1 families from a population (C3) advanced from the same base (CO) population by using replicated yield tests in each cycle [IAP4R(S1)C3]. Our objectives were to compare the performance in C3 of families developed by using each selection strategy and to assess the genetic variability among S_1 families. Sixty S_1 families from each population were grown in five Iowa environments.

Mean grain yields of S_1 families derived from IAP1R(M)C3 and IAP4R(S1)C3 were not significantly different (beyond P>0.05). Estimates of genetic variance among families (σ_c^2) from IAP4R(S1)C3 were significantly greater for seeds/panicle and days to midbloom, but σ_g^2 was not significantly different from IAP1R(M)C3 for grain yield, panicles/plant, and plant height. Greater σ_g^2 for 100-seed weight was observed among the S_1 familes from IAP1R(M)C3. Except for 100-seed weight, heritability estimates for agronomic characters were not significantly different for the two populations.

Considerations of mass selection and S_1 testing should be made in relation to gains per season and use of project resources. On a perseason basis, mass selection seems preferable because S_1 testing requires three seasons per cycle versus one for mass selection. If off-season nurseries are used for recombination of testing units, gain per year from S_1 testing would be similar or superior to that from mass selection. INDEX DESCRIPTORS: Sorghum bicolor L. Moench, breeding systems, random-mating populations, agronomic traits.

The incorporation of genetic male sterility into sorghum [Sorghum bicolor (L.) Moench] breeding populations has allowed sorghum breeders to take advantage of recurrent selection schemes. Because additive genetic variance is the major genetic component in the expression of many characters in sorghum, each increment of improvement at the population level also should improve inbreds and hybrids derived from the population.

Mass selection (phenotypic recurrent selection) of individual plants is a simple, relatively low-cost method of population improvement. It has been used effectively in sorghum for characters that are highly heritable (Doggett, 1968). A method of recurrent selection in sorghum that used replicated yield tests of S_1 lines was described by Doggett and Eberhart (1968). Theoretically, the improvement of quantitatively inherited traits by using S_1 testing should be greater than that from mass selection (Eberhart, 1972; Empig et al., 1971; Hallauer and Miranda, 1988).

The following report compares the performance of two randommating populations of sorghum that were derived from the same base (C0) population. IAP1R(M)C3 was developed by using mass selection for individual-panicle grain weight (Atkins, 1980), whereas IAP4R(S1)C3 was developed by using replicated tests for grain yield of S₁ families (Atkins, 1986). Our objectives were to (i) compare the performance in C3 of lines developed by using each selection stategy, (ii) assess the genetic variability among S₁ families derived from C3 of each population, and (iii) estimate the magnitude of correlated changes among agronomic traits.

MATERIALS AND METHODS

The random-mating population IAP1R-C0 was developed by crossing 10 lines that restore pollen fertility in A1 cytoplasm (R-lines) to male-sterile ($ms_3 ms_3$) segregates of an existing unrelated population, NP3R (Nordquist et al., 1973). The lines used were Tx7078, Tx7000 ('Caprock'), Tx2536, NB9040; Iowa selections from the temperate bulk of IS2403C, IS3063C, IS12567C, and IS12608C; plus Iowa selections of 'Redbine 58' × Ak9-2, and 'Redlan' × OKY7. The mass- and S₁-selected families used in our experiments stemmed from that base (C0) population.

To advance the population by mass selection for panicle weight, 30 equal rectangular grids (5 rows, 6.08 m long) were superimposed in each cycle on an isolation planting of approximately 6,000 plants (30 rows, 30.4 m long, and 1.02 m apart) near Ames, Iowa. All plants in the base population were male fertile $(Ms_3 ms_3)$. Panicles borne on the main culm were tagged at anthesis, and 15 to 25 tagged plants per grid were harvested. Selection was for desirable plant height (100-150 cm), for medium to large panicles, and against extremely late maturity. Selected panicles were threshed individually, and the 10 panicles with the heaviest grain weight were chosen from each grid to provide seed for the next cycle of IAP1R(M). Equal amounts of seed by weight from the 300 selected panicles were composited to plant the second isolation block (C1). Male-sterile segregates (m_3, m_3, m_3) were tagged at anthesis in C1 and all following cycles. After three cycles of mass selection on an individual panicle basis for grain weight, the seed produced was designated IAP1R(M)C3.

The second method of population advancement was based on the results of replicated yield tests of S_1 families. In the first year, fertile panicles were selected from the CO isolation planting as described previously. In the second year, seed from each selected panicle was planted in a single 1.82 m row. Selection was made among those rows for desirable plant height (100-150 cm) and good agronomic type. Within each selected row, the best fertile panicle was chosen visually for inclusion in the yield trial. In the third year, a yield test of the S_1 families was conducted at the Agronomy and Agricultural Engineering Research Center near Ames, Iowa, in single-row plots, 4.26 m long, spaced 1.02 m apart, arranged in a simple-lattice design with two replicates. On the basis of grain yields from that test, remnant seed from the individual panicles selected from the previous isolation block was composited to form the next cycle (C1). Eighteen percent of the entries included in each yield trial were selected to make up each succeeding cycle. The male-sterility gene segregated in C1 and seed set on male-sterile panicles was used to constitute C2 and C3. After three cycles of S1 yield testing, seed produced in the isolated planting was released as IAP4R(S1)C3. The progression of IAP4R(S1)C1 through C3 is described in Table 1.

Seed of 60 S_1 families chosen randomly from the third cycle isolation planting of each population was used to plant our experi-

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No. of panicles planted from previous isolation	No. of panicles planted in yield test	No. of entries selected from yield test for next isolation planting	Cycle of of next isolation planting	
648 (fertile)	196	35	C1	
540 (male sterile)	169	30	C2	
427 (male sterile)	144	26	C 3	

Table 1. Procedure used for advancing the sorghum population IAP4R(S1) through three cycles of selection.

ments. Yield trials were planted 4 June 1985, 21 May 1986, 22 May 1987, and 25 May 1988 at the Agronomy and Agricultural Engineering Research Center near Ames, Iowa, and 9 June 1987 at the Burkey Research Farm, also near Ames. Experimental sites at the Agronomy Research Center were fertilized before planting with 134 kg/ha of N, but nitrogen was not applied to the test area at the Burkey Farm. Applications of 67 kg/ha of P_2O_5 and K_2O) for each test were made the preceding autumn. The soil type at both locations was Nicollet (fine-loamy, mixed, mesic Aquic Hapludoll).

A replication-in-block field design (Schutz and Cockerham, 1966) was used in each environment. Ten S₁ families from each population were included in each of six groups, with two replicates of a group per block. Individual plots were single rows 4.27 m long with 1.02 m between rows. Seedlings in the row were thinned to 10 cm apart (97,000 plants/ha). Data were obtained in all environments 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 from dry panicle weight by using the procedure described by Robinson and Bernat (1963). Additional characters calculated from these data were panicles/plant and seeds/panicle. Data were recorded for plant height in 1986 through 1988, and for days to midbloom (planting to 50% anthesis) in 1987 and 1988.

All effects, except those attributable to selection methods were considered random in the combined analyses of variance. Genotypes (S₁ families) and environments (year/location) were considered random for estimation of the variance components σ^2 (error variance), σ^2_{ge} (gentoype-environment interaction variance), and σ^2_g (genetic variance). Standards errors (SE) of the variance components were computed by using the formula presented by Searle (1971, p. 416). Heritabilities (h²) and their SE were estimated by using formulas presented by Hallauer and Miranda (1988, p. 90-91). Phenotypic correlations (r_{ph}) between pairs of traits were calculated by using the formula:

$$r_g = \frac{\sigma_{gxy,}}{\sqrt{\sigma_{gx}^2 \sigma_{gy}^2}}$$

where $\sigma_{gxy} = genetic$ covariance between traits x and y, $\sigma_{gx}^2 = S_1$ family genetic variance for trait x, and $\sigma_{gy}^2 = S_1$ family genetic variance for trait y.

RESULTS

Dry soil at Ames in 1985 delayed planting, and sparse rainfall throughout the summer resulted in an average grain yield of 4.45 Mg/ ha. Low temperatures after planting in 1986 caused slow emergence of seedlings, but environmental conditions were favorable through the rest of the season, resulting in a mean yield of 5.27 Mg/ha. In 1987, warm temperatures and ample summer rainfall produced mean yields of 5.60 Mg/ha for the Ames test and 5.43 Mg/ha at the Burkey Farm. The 1988 Ames test had the highest average yield, 5.71 Mg/ha, despite very high temperatures and limited (but timely) rainfall.

Mean grain yields (Table 2) of the S₁ families derived from IAP1R(M)C3 and IAP4R(S1)C3 were not significantly different (beyond P>0.05). S₁ families from IAP1R(M)C3 (hereafter called M) yielded significantly (P<0.01) more than those from IAP4R(S1)C3 (hereafter called S₁) in the 1987 Burkey Farm test, but significantly (P<0.01) less in the 1988 Ames test. There were no significant yield differences (P<0.05) between families from the populations in the other environments (individual location data not shown). Both populations produced three S₁ families that had mean yields greater than 6.00 Mg/ha.

High and low family values (Table 2) for grain yield and other agronomic traits suggested there was significant variability for these traits among the S_1 families from both populations. Overall, and in each environment, the S_1 families from M averaged fewer seeds/panicle, but larger seed and more panicles/plant than those from S_1 . Means for the individual and combined environments also showed that the M population was taller than S_1 and it required fewer days to reach midbloom stage.

Estimates of variance components in Table 3 indicated that the genetic variance (σ_g^2) among S₁ families from S₁ populaton was significantly greater (P<0.05) than M for seeds/panicle and days to midbloom, but σ_g^2 was not significantly different from M for grain yield, panicles/plant and plant height. Greater genetic variance for 100-seed weight was observed among the S₁ families for M population. Compared with M, the S₁ population had significantly larger estimates for the genotype \times environment interaction component (σ_{ge}^2) for grain yield, seeds/panicle, and 100-seed weight and a significantly smaller estimate for plant height. Estimates of σ_{ge}^2 were small relative to error and genetic variance for all traits in both populations.

Except for heritability of 100-seed weight on a plot basis (Table 3), h² values for agronomic characters in the two populations were not significantly different from each other. Heritabilities on a progeny mean basis were relatively high for all traits, reflecting the small effect of the genotype \times environment variance and the good growing conditions. High heritabilities for plant height and days to midbloom reflect the large genetic component in relation to error variance and σ_{re}^2 .

 σ_{ge}^2 . Phenotypic correlations among agronomic characters were similar for S₁ families derived from M and S₁ populations (Table 4). Coefficients were positive and significant for grain yield with seeds/panicles and plant height, and for seeds/panicle with days to midbloom. Significant negative correlations occurred in both populations for seeds/panicle with 100-seed weight and panicles/plant. Phenotypic correlations smaller than ± 0.50 have coefficients of determination below 25%, meaning that they account for less than one-fourth of the observed variation. Only the correlation of seeds/panicle vs. 100-seed weight had coefficients $\geq \pm 0.50$ in both populations. The largest differences between phenotypic correlations for the M and S₁ populations were for 100-seed weight vs. plant height, 100-seed weight vs. days to midbloom, and panicles/plant vs. plant height. Genotypic and phenotypic correlation coefficients were nearly similar for most trait comparisons.

			Statistic		
Character	Population	Mean	Low family value	High family value	F test [†] M mean vs. S ₁ mean
Grain yield (Mg/ha)	М	5.33 ± 0.04	4.12	6.58	
	S ₁	5.26 ± 0.04	4.12	6.28	
Seeds/panicle	Ň	1288 ± 13	709	1945	
•	S ₁	1566 ± 17	1031	2334	**
100-seed weight (g)	M	2.61 ± 0.02	1.99	3.27	
0 0	S ₁	2.32 ± 0.02	1.88	2.79	**
Panicles/plant	Ń	1.81 ± 0.01	1.52	2.26	
•	S ₁	1.67 ± 0.01	1.35	2.07	**
Plant height (cm)‡	M	143 ± 1	115	174	
	S ₁	129 ± 1	105	161	**
Days to midbloom §	M	61.4 ± 0.2	56.5	68.3	
·	S ₁	67.5 ± 0.2	58.8	73.7	**

Table 2. Means, standard errors, low and high family values, and levels of significance for characters measured on S_1 families from IAP1R(M)C3 and IAP4R(S1)C3 sorghum populations at Ames, Iowa, during 1985-88.

†, ** Differences significant beyond P>0.01.

‡ Not measured in 1985.

§ Not recorded in 1985 and 1986.

DISCUSSION

Average grain yield of S_1 families derived from M and S_1 populations did not differ significantly, and distributions of yields of families from the two populations were similar. Ess and Atkins (1989) compared the performance of hybrids formed by using S_1 families derived from IAPIR(M)C3 and IAP4R(S1)C3 and did not find significant differences for grain yield between the two sets of hybrids. In our experiments, means of S_1 families from C3 of the two populations exhibited significant differences for all other traits measured. The largest percentage-difference between population means was for seeds/ panicle, and the number of S₁ families producing more than 1,500 seeds/panicle was greater for IAP4R(S1)C3. For days to midbloom, the number of late-maturing families was greater for S₁. Mean days to midbloom for S₁ was nearly a week later than the average for IAP1R(M)c3. Means for the S₁ families from M for plant height, 100-seed weight, and panicles/plant, reflected the fact that they were generally taller and produced heavier seed and more panicles/plant compared with families from S₁.

Relative proportions of genetic, genotype x environment, and error variances are important in the planning of breeding strategies. For

Table 3. Estimates of components of variance and heritability and their standard errors determined from the combined analysis of S_1 familes from IAP1R(M)C3 and IAP4R(S1)C3 sorghum populations grown at Ames, Iowa, during 1985-88.

								Heritability (h ²)		
		Variance component				_				
Character	Population	σ^2		σ_{ge}^2		σ_g^2		Progeny mea basis	Plot basis	
Grain yield (Mg/ha)	M S ₁	0.237 0.222	$\pm 0.014 \\ \pm 0.013$	0.059 0.099*	$\pm 0.017 \\ \pm 0.020$	0.191 0.202	$\pm 0.043 \\ \pm 0.046$	$\begin{array}{c} 0.84 \ \pm \ 0.19 \\ 0.83 \ \pm \ 0.19 \end{array}$	$\begin{array}{rrr} 0.39 & \pm 0.09 \\ 0.39 & \pm 0.09 \end{array}$	
Seeds/panicle	M S ₁	36746 54354*	± 2220 ± 3284	4439 15048*	± 2275 ± 4026	34301 60315*	± 7345 ± 12994	$\begin{array}{c} 0.88 \ \pm \ 0.19 \\ 0.88 \ \pm \ 0.19 \end{array}$	$\begin{array}{rrr} 0.45 & \pm \ 0.10 \\ 0.46 & \pm \ 0.10 \end{array}$	
100-seed weight (g)	M S ₁	$\begin{array}{c} 0.074 \\ 0.081 \end{array}$	$\pm 0.005 \\ \pm 0.005$	0.009 0.034*	$\pm 0.005 \\ \pm 0.007$	0.065* 0.040	$\pm 0.014 \\ \pm 0.010$	$\begin{array}{c} 0.88 \ \pm \ 0.19 \\ 0.73 \ \pm \ 0.19 \end{array}$	$\begin{array}{c} 0.44^{*} \pm 0.09 \\ 0.26 \ \pm 0.07 \end{array}$	
Panicles/plant	M S ₁	0.038 * 0.027	$\pm 0.002 \\ \pm 0.002$	0.009 0.004	± 0.003 ± 0.002	0.024 0.022	$\pm 0.006 \\ \pm 0.005$	$\begin{array}{c} 0.81 \ \pm \ 0.19 \\ 0.87 \ \pm \ 0.19 \end{array}$	$\begin{array}{rrr} 0.33 & \pm \ 0.08 \\ 0.42 & \pm \ 0.09 \end{array}$	
Plant height (cm)†	\mathbf{M} \mathbf{S}_1	100.8* 54.5	$\pm 6.8 \\ \pm 3.7$	20.0* 7.5	$\pm 7.7 \pm 3.8$	151.9 128.9	± 25.6 ± 20.8	$\begin{array}{r} 0.92 \ \pm \ 0.15 \\ 0.95 \ \pm \ 0.15 \end{array}$	$\begin{array}{rrr} 0.56 & \pm \ 0.09 \\ 0.68 & \pm \ 0.11 \end{array}$	
Days to midbloom‡	M S ₁	2.70 2.40	± 0.21 ± 0.19	1.27 1.16	$\pm 0.35 \\ \pm 0.31$	6.55 9.39*	± 0.84 ± 1.15	$\begin{array}{c} 0.93 \ \pm \ 0.11 \\ 0.95 \ \pm \ 0.11 \end{array}$	$\begin{array}{rrr} 0.62 & \pm 0.08 \\ 0.73 & \pm 0.09 \end{array}$	

* The significantly higher component of variance for M vs. S1 comparison; i.e., difference is more than twice the standard error.

[†] Not measured in 1985.

[‡] Not recorded in 1985 and 1986.

Table 4. Phenotypic (above diagonal) and genotypic (below diagonal) coefficients of correlation among traits determined from the combined analysis of S_1 families for IAPIR(M)C3 and IAP4R(S1)C3 sorghum populations grown at Ames, Iowa, during 1985-88.

Character	Population	Grain yield	Seeds/ panicle	100-seed weight	Panicles/ plant	Plant height	Days to midbloom
Grain yield	M S.		0.44**	-0.05	0.27*	0.32*	0.10
Seeds/panicle	M S ₁	0.47 0.57		-0.76** -0.64**	-0.48** -0.42**	-0.10 0.01	0.49** 0.38**
100-seed weight	M S.	-0.08	-0.77 -0.64	0.01	0.20	0.17	-0.38** -0.03
Panicles/plant	M S.	0.25	-0.52 -0.45	0.24	0.07	0.37**	-0.26*
Plant height †	M S	0.37	-0.14 0.00	0.21	0.48 0.05	0.09	-0.01
Days to midbloom‡	M S ₁	0.18 0.21	0.68	-0.52 -0.06	-0.37 -0.21	-0.04 -0.01	

*,** Significant beyond P<0.05 and P<0.01, respectively.

† Not measured in 1985.

‡Not recorded in 1985 and 1986.

both C3 populations, estimates of genetic variances among S_1 families were significantly greater than zero (i.e., two times the standard error) for all traits (Table 3), indicating that recurrent selection should be effective. Estimates of error variance in both populations were similar to the estimates of genetic variance for grain yield, seeds/panicles, and panicles/plant, suggesting that the extent and precision of measurement should be considered as well in evaluations of these traits. For plant height and days to midbloom, the estimates of genetic variance in both populations were large compared with estimates of error, and genotype x environment variances. Precise evaluations for height and midbloom should be possible by using relatively few environments.

Genetic variances for grain yield among the S_1 families from M and S_1 did not differ significantly in our experiments. The genetic variances for seeds/panicle and days to midbloom were greater among families from S_1 and greater for 100-seed weight in M population. Ess and Atkins (1989) reported similarly that genetic variances for grain yield among hybrids formed from male parents derived from IAP1R(M)C3 and IAP4R(S1)C3 were not significantly different. For the other traits measured, their estimates of genetic variances among the sets of hybrids were either alike or they were greater for the hybrids with male parents derived from M. In our studies neither selection method altered genetic variance among C3 genotypes markedly in relation to the other. The results are encouraging because there seems to be adequate genetic variability for further selection progress and improvement of grain yield in either population.

Heritability estimates for grain yield on a progeny-mean basis were 0.84 for M and 0.83 for S_1 . These estimates are similar to the values of 0.74, 0.84, and 0.85 reported by Lothrop et al. (1985a) for S_1 and half-sib families in their study of IAP1R(M)C3. Ess and Atkins (1989) reported heritabilities of 0.67 and 0.56 for yield among hybrids formed by using S_1 families from IAP1R(M)C3 and IAP4R(S1)C3. The heritability of yield on a progeny mean basis ranged from 0.58 to 0.87 in other studies with random-mating populations of sorghum (Kwolek et al., 1986; Eckebil et al., 1977; Jan-orn et al., 1976).

Different characters may be correlated because they are influenced by genes that effect both characters (pleiotropy) or because they are influenced by different genes linked on the same chromosome (linkage). Regardless of the cause, the magnitude of genotypic correlation between traits will have an impact on response to selection (Baker, 1986). Ross et al. (1981) suggested that, if linkage is involved, continued random mating should increase the opportunities for overcoming unfavorable genetic correlations. Seeds/panicle and plant height showed highest correlation with grain yield with either selection method. Lothrop et al. (1985b), Jan-orn et al. (1976), and Koraiem et al. (1979) also found those traits most highly associated with grain yield. Negative genetic correlations (Table 4) of seeds/ panicle with 100-seed weight and panicles/plant point to a strong genetic tendency for yield component compensation in both populations. The means in Table 2 suggest that while seeds/panicle was increased in S₁ relative to M, decreases in S₁ for 100-seed weight and panicles/plant offset the seeds/panicle component so that yield of the population S₁ did not differ significantly from M.

Regression analyses of data from supplementary experiments with C0 through C3 composites of S₁ and half-sib families (Secrist, 1989) did not distinguish a different type of response for IAP1R(M)C3 vs. IAP4R(S1)C3 for grain yield, any yield component, or plant height, in association with increased yield over cycles. In those analyses, the regression coefficient for grain yield for S₁ testing, 0.170 Mg/ha per cycle, was not significantly different from the increase of 0.117 Mg/ha per cycle observed for mass selection. Days to midbloom was the only trait that showed significantly different (P<0.01) regression coefficients for the two populations. S₁ testing resulted in a population that was significantly (P<0.01) later to midbloom, by 1.67 days per cycle, while mass selection resulted in a population that was significantly (P<0.01) earlier by one-third of a day per cycle.

Results from our study, together with those of Ess and Atkins (1989), do not provide a clear choice for mass selection vs. S_1 -testing recurrent selection. Both methods improved grain yield of advanced-cycle composites relative to the base (C0) population (Secrist, 1989). But mean grain yields of S_1 families derived from C3 of the populations were not significantly different in our experiments. It seems most appropriate to evaluate the selection procedures in terms of gain for season, or gain per year, and in relation to use of project resources. On a per-season basis, mass selection seems preferable becase S_1 testing requires three seasons per cycle whereas mass selection requires only one. If only one growing season per year is available to the breeder, mass selection would be a likely choice. But if off-season nurseries are used for recombination and/or development of testing units (S_1 familes), gain per year from S_1 testing should be similar to that from mass selection.

Mass selection to improve grain yield may be most appropriate in early stages of population development, when incorporation of diverse germplasm and subsequent breaking of linkage groups through intermating is most important. Mass selection also may be used in initial cycles of a recurrent selection program to select for traits that have relatively high heritability. Once the genetic variability for those traits is reduced, the breeder could change the evaluation procedure to some type of progeny testing (Hallauer, 1986). S₁ testing may be utilized in later stages of population development when the breeder wishes to maintain desirable linkage groups and generate families that will contribute directly to the development of cultivars and hybrids.

 S_1 testing can be very effective for improving grain yield in a population, but the gains must be balanced against increased demands for land, labor, and time. With a given amount of resources, a breeder can evaluate fewer selections in a S_1 testing program compared with a program based on mass selection. To increase selection intensity, a breeder may select for highly-heritable traits before conducting expensive yield trials. Undesirable increases in plant height and days to midbloom, which are common in populations improved by using recurrent selection, may be reduced by selecting plants with desirable height and maturity before S_1 testing is initiated (Ross, 1978). Elimination of plants based on qualitative characteristics, however, may restrict grain yield improvement because of unfavorable genetic correlation between the qualitative trait and grain yield (Hallauer, 1987; Hallauer and Sears, 1969).

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