Kwolek, Thomas Frank

COMPARISONS OF AGRONOMIC TRAITS IN THE INITIAL AND ADVANCED CYCLES OF IAP3BR(M) RANDOM-MATING GRAIN SORGHUM POPULATION

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Comparisons of agronomic traits in the initial and advanced cycles of IAP3BR(M) random-mating grain sorghum population

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Thomas Frank Kwolek

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INTRODUCTION

The potential benefits from increasing seed size in sorghum [Sorghum bicolor (L.) Moench] make it an important character for sorghum breeders to consider in an improvement program. The potential benefits include indirect increases in grain yield, because seed size is one of the primary components of yield. Additionally, there may be increases in germination percentages and improved stand establishment associated with large-seeded genotypes.

Gridded mass selection is an effective method for improving quantitatively inherited characters that are controlled primarily by additive gene action. Recurrent selection in genetically diverse populations should provide sorghum breeders with a fruitful means for generating new germplasm pools and allow greater utilization of the inherent variability that is present in sorghums around the world.

The development of IAP3BR random-mating sorghum population was initiated in 1976 to provide a germplasm source for large-seeded genotypes. Thirty large-seeded B-lines (nonrestorer in A_1 cytoplasm) or R-lines (fertility restorer in A_1 cytoplasm) were crossed onto male-sterile panicles of an existing population, IAP1R(M)C1. The 30 parental lines were the most desirable agronomic types among 116 large-seeded genotypes obtained from sorghum breeders in 10 states.

The purpose of my research was to evaluate changes in the breeding potential of IAP3BR(M) after four cycles of gridded mass selection for heavy 100-seed weight (large seed). Characters analyzed were grain yield, 100-seed weight, seeds/panicle, panicles/plant, days to midbloom, plant height, and panicle type. Experiment I examined trends, means, and estimated inbreeding depression among S_1 and half-sib (HS) bulk composites over four cycles of selection. In Experiment II, population means, variances, and heritabilities were estimated for the initial (C0) and an advanced cycle (C4). Phenotypic and genetic correlations among characters were also calculated for the two cycles. Additionally, estimates of expected gains were obtained for most characters in the two cycles for S_1 family selection and gridded mass selection, and correlated responses among the characters to S_1 family selection were determined.

LITERATURE REVIEW

Recurrent Selection in Sorghum

Recurrent selection has become a valuable tool in sorghum breeding since the first sorghum random-mating population, NP1BR, was constituted by O. J. Webster in 1960 (Nordquist et al., 1973). Ross et al. (1971) summarized the theory underlying population improvement in sorghum. Briefly, it involves the selection and recombination of superior individuals to form an elite population, with a cycling or repetition of the selection and recombination phases. If random-mating and selection is effective, the population mean for the character under selection should shift favorably while maintaining the genetic variability of the initial cycle for all characters. As recurrent selection continues, it should be possible to isolate superior genotypes in larger numbers. In addition to increasing the frequency of favorable alleles, there is opportunity for the breakage of close linkages that might not occur in a conventional breeding program that is based on inbreeding and pedigree selection.

Doggett (1972b) stated that recurrent selection could lead the plant breeder away from working with very restricted, elite materials, therefore utilizing more of the total variability that is available in a given species. Further, Doggett (1972a) found that recurrent selection releases concealed

variability through recombination and exposes the released variability through selection. Gardner (1972) concluded that recurrent selection should result in improved genotypes, with each cycle of improvement providing opportunity to develop new inbreds or open-pollinated varieties. The degree of success, however, will depend upon the genetic variability in the base population.

Before random-mating in sorghums could be accomplished readily, it was necessary to introduce male-sterility into parental lines or populations, using either a cytoplasmic or genetic system. Nine male-sterility systems have been identified in sorghums, but only three genetic male-steriles, $\underline{ms}_3$, $\underline{ms}_7$, and $\underline{al}$, have been used extensively (Ross et al., 1971). With male-sterility, outcrossing is enforced and population development can begin. Ross (1973) discussed two methods for the initial synthesis of breeding materials: (1) populations can be developed by backcrossing the genetic male-sterility into component lines, and then intermating the derived backcrosses in a diallel fashion to produce the initial cycle, or (2) cross selected lines to male-sterile segregates of an existing population. Then, by using backcross procedures, the desired percentages of new germplasm compared to the existing population can be adjusted. Several intra- and interpopulation breeding methods for sorghum have been described and their features summarized by Ross et al.

(1971) and Ross (1973). These are mass selection, half-sib family selection, full-sib selection, S_1 progeny testing, and reciprocal recurrent selection.

Mass Selection

Mass selection for the improvement of many species undoubtedly dates to the time of initial domestication of plants. Gardner (1961) conducted mass selection for grain yield of maize (Zea mays L.). He concluded that the use of mass selection of individual plants, because of the simplicity and apparent effectiveness, would be a good method for yield improvement. In addition, mass selection would increase the frequency of favorable alleles in the population, thereby enhancing the population's potential as a source of lines for inbreeding and hybrid development.

In Gardner's (1961) experiment, another precaution was taken to increase the efficiency of mass selection. The fields in which selection was conducted were stratified into grids with equal-size cells. High yielding plants were harvested from each of the grids in an attempt to reduce the effects of environmental variation between plants and increase selection efficiency. In a subsequent paper, Lonnquist et al. (1966) reported that estimates of genetic variance in the maize population Hays Golden, after six cycles of gridded mass selection, showed no decline in the additive genetic

variance, indicating that continued gains could be expected for grain yield.

Mass selection may be a better procedure when economic considerations such as a single crop per year and limited funding hamper a breeding program. Mass selection does have specific applications to population improvement when the trait under consideration is known to be highly heritable. Ross et al. (1971) suggested that mass selection in sorghum should be effective for screening large numbers of plants for disease or insect resistance, environmental tolerances (e.g., alkaline or acidic soils) or for grain quality factors (e.g., protein or oil percentage).

Doggett and Eberhart (1968) concluded that S_1 family testing has many advantages as a breeding procedure, and it usually results in good progress from selection. In more recent studies, Jan-Orn et al. (1976) used data from 196 half-sib, 196 full-sib, and 196 S_1 families of the sorghum population NP3R to estimate variance components and predict gains from selection. The predicted response from single-trait selection was highest for S_1 family selection for most traits. Highly heritable traits that are controlled primarily by additive gene action (e.g., maturity and plant height), however, could be improved by mass selection. These results were supported by Lothrop (1983). His experiments with the sorghum population IAP1R showed that gains may be slow for

traits that have low heritability or when selection is based on individual plants. Additionally, he found that genotype by environment interactions made selection at one central location of little value in improving performance over a wider area. Because 100-seed weight was controlled primarily by additive gene effects and showed a small genotype by environment interaction, gridded mass selection was shown to be effective for improving that trait.

Doggett (1968) elaborated on the features of mass selection when male-sterile heads are harvested and the gain from selection, G, equals $k(\frac{1}{2})\sigma_A^2/\sigma_{ph}$. He proposed alternating male-sterile and fertile plant mass selection in which fertile plant mass selection produces gains of $G = k\sigma_A^2/\sigma_{ph}$ in one season and male-sterile plant selection produces gains of $G = k(\frac{1}{2})\sigma_A^2/\sigma_{ph}$ in the next. He suggested that this system was good for areas such as Serere, Uganda, where rainfall patterns produce two growing seasons in a single year.

Mass selection by recombining male-sterile heads, mass selection by recombining male-sterile and fertile heads in alternating seasons, and S_1 family testing were compared in additional experiments with sorghums by Doggett (1972b). For grain yield, he obtained increases of 8% for male-sterile selection, 19% for the alternating system, and 25% for S_1 family testing. He concluded that, if resources permit, S_1 family testing would be the best system for improving grain yield.

Sorghum Plant and Grain Development

Grain yield per plant in sorghum can be divided into three primary components: the number of panicles/plant, the number of seeds/panicle, and the size of the seed. Eastin (1972) described plant development in sorghum in three stages: GS1, sowing to panicle initiation; GS2, panicle initiation to anthesis; and GS3, anthesis to maturity. Vanderlip and Reeves (1972) examined growth stages in the sorghum hybrid RS610. They found that the number of panicles/plant generally is determined in the first 30 days after emergence, because at this stage, the apical meristem changes from a vegetative to reproductive phase. This stage includes the tillering processes (Freeman, 1970), but may or may not include axillary buds that are higher on the culm. The axillary buds generally appear as a result of environmental stimuli, only after the panicle on the main stem has emerged from the flagleaf (Artschwager, 1948). Pauli et al. (1964) found that the time from planting to growing-point differentiation was about one-third of the time required for physiological maturity, regardless of variety or planting date. They also determined that the time from floral initiation to half-bloom was approximately one-third of the time from emergence to physiological maturity.

Vanderlip and Reeves (1972), in studies that used the hybrid RS610, found that half-bloom occurred in 60 days and

physiological maturity in 95 days from emergence. The number of seeds/panicle was determined during GS2 and was dependent on the number of florets initiated and the percentage that were pollinated and fertilized. Lee et al. (1974) presented an in-depth description of GS2. They concluded that three factors control grain yield during the second stage of growth: (1) number of primary branch primordia, (2) number of branches from each primary branch, and (3) the timing of spikelet differentiation. Eastin (1972) found that during GS2, the maximum potential seed is set with the actual number that develop dependent on subsequent environmental conditions.

To explain this finding, Muchow and Wilson (1976) proposed that, in the normal course of development, more fertile spikelets are initiated than can develop into "normal" sized kernels, and adjustment of seed numbers occurs later to bring the storage and supply of nutrients into balance. This phenomenon may serve to explain the consistency of kernel size within a genotype.

The time period from fertilization to maturity is termed the grain-filling period (i.e., the time when seed size is determined). Dickinson (1976) observed that grain growth in sorghum progresses in a linear manner, beginning two to three days after anthesis and continuing until two days before black layer formation. He also found that seed size was most sensitive to high temperatures six to nine days after anthesis,

corresponding to a period when seed volume potential was determined. Dickinson also ascertained that the formation of cellular structures in sorghum may limit seed size, not only by the number of endosperm cells produced but by the cell wall plasticity inherent in these cells.

Maximum dry weight and physiological maturity of sorghum seed corresponds with the development of a black layer similar to that in maize, according to Eastin et al. (1973) and McBee et al. (1983). Eastin et al. (1976) using two cool-tolerant and one temperate-zone sorghum genotypes conducted experiments where temperatures were elevated 5°C above the level considered optimum for growth during GS2 and GS3. This treatment reduced grain yields 25 to 36%. However, the yield reduction was associated with reduced seed numbers and not seed size, indicating that seed size was quite stable. Unfortunately, in the sorghum literature there is a lack of information on the relationship between seed size and black layer formation, and also on the length and rate of grain fill (Eastin, 1981). Using the sorghum hybrid RS610, Chowdhury and Wardlaw (1978) concluded that the duration of grain growth was independent of filling rate and that the completion of grain filling was not brought about by attainment of a particular seed size.

Seed formation in most cereal grain crops is very similar. Dure (1975) concluded that the cereal species make little attempt to store much of their nutrient reserve in the

embryo, other than a small amount of oil that is found in the scutellum. Carbohydrates tend to be polymerized in the endosperm, while protein is accumulated in the testa and aluerone layers. Hubbard et al. (1950) analyzed five varieties of sorghum and found that the endosperm ranged from 80.0 to 84.6% of the total seed weight, germ ranged from 7.8 to 12.1%, and bran from 7.3 to 9.3%. They also stated that sorghum closely resembled maize in the proportion of starch, protein, and oil, but made no conclusion as to how variations in these proportions might influence seed size. Little distinction was made between seed weight per unit (e.g., 100-seeds) and seed size in most studies. Ayyanger et al. (1938) found seed weight per unit to be a reliable indicator of seed size due to the high positive correlation between the two traits.

Seed Size Studies in Sorghum

The potential benefits from increasing seed size make it an important trait for sorghum breeders to consider in an improvement program. Bartel and Martin (1938) observed that large sorghum seeds produce large seedlings that seem to grow rapidly in the early growth stages. However, Swanson and Hunter (1936) found seed of some sorghum varieties showed inherently better ability to germinate due in part to the relative thickness of the starchy mesocarp layer of cells

located in the seedcoat. Further, they concluded that seed size was not a factor from the standpoint of food reserves because small-seeded varieties tended to display higher germination percentages than did the large-seeded varieties. Kersting et al. (1961) found large positive correlations for percentage germination with 100-seed weight, but there was little variation in percentage germination if all seeds in the seedlot had reached maximum dry weight. Similarly, Suh et al. (1974) found that sorghums from two different seedlots (based on weight per unit) did not differ significantly for several agronomic characters.

In two studies of the nature of heterosis, Arnon and Blum (1962) and Kambal and Webster (1966) found that the yield advantage of sorghum hybrids over the mean of their parents resulted mainly from increased seeds/panicle, but additionally, from increases in seed size. Malm (1968) found that sorghum hybrids, which involved large-seeded exotic lines as male parents, produced higher yields than those hybrids which used the same set of female parents but had an adapted male parent, TX7078. He suggested that, by using similar exotic materials and selecting for increased seed size, a breeder should make significant gains in grain yield. Large-seeded sorghums also are thought to be desirable for livestock feeding and for milling purposes (Quinby and Schertz, 1970). Heinrich et al. (1983) found that large-seeded sorghum genotypes tended to be

stable across environments. They concluded seed weight per unit may be an important factor in both the level and stability of grain yield.

The inheritance of seed size or seed weight per unit in sorghum is considered to be quantitative in nature. Hayes and Garber (1927) examined the F_2 generation progeny of the cross Red Amber x Feterita and found the distribution of seed size to be: 337 small, 2025 intermediate, and 286 large seed. They concluded that the F_2 segregation was typical of the inheritance of a character that is dependent on several factors for its expression. Voigt et al. (1966) crossed Big Seed, a large-seeded variety, by Norghum, a small-seeded variety, and examined seeds from plants of the parents, F_1, F_2, and the first two backcross generations. Their conclusion was that a minimum of three or four genetic factors or blocks of genes controlled seed size.

Large differences in seed size exist in the world collections of sorghum. Swarup and Chaugale (1962) found a range of 0.97 to 3.50 g/100 seeds among the 70 varieties that they surveyed. In a larger group of materials, Miller (1968) recorded a range of 0.70 to 6.10 g/100 seeds among 585 exotic genotypes. However, Quinby and Schertz (1970) reported that most sorghum hybrids have about the same seed size, indicating little diversity among the parents used currently in commercial hybrids. The large amount of diversity available from

several sources, however, has encouraged studies to determine how much of the variability is genetic and of potential use to sorghum breeders.

Investigations with Narrow-Base Populations

Many studies have been conducted by researchers using populations that have a narrow genetic base to provide estimates of general combining ability (GCA) and specific combining ability (SCA). GCA provides an indication of the extent of additive gene action, while SCA estimates the impact of nonadditive effects on the expression of a given character.

Kambal and Webster (1965) used 10 sorghum A-lines and 19 R-lines, considered representative of those available in 1958 for the production of grain-type hybrids in the United States, to produce 190 F_1s. They found highly significant variation in both GCA and SCA for 1000-seed weight with a GCA/SCA ratio of 11:1. In addition, they reported that both GCA and SCA for seed size were stable over environments, indicating that testing would not be necessary over a large number of locations.

Hybrids from an eight-inbred parent diallel were used in experiments reported by Niehaus and Pickett (1966). Five of the parental lines were standard, combine-height sorghums, and three were recent introductions. GCA and SCA effects were highly significant in both the F_1 and F_2 generations for seed

size, with GCA/SCA ratios in the F_1 and F_2 of 0.6:1 and 0.9:1, respectively. They concluded that SCA effects were more important than GCA effects for the expression of seed size in that population.

Voigt et al. (1966) studied the cross of Big Seed x Norghum using the parents, their F_1 and F_2 generations, and the first two backcrosses and concluded that seed size was controlled primarily by genes that were additive in their effect. They found little evidence that dominance or epistasis contributed to the inheritance of seed size. A ratio of 10:1 for additive vs dominance genetic variance was calculated and heritability for seed size was estimated at 60%. These findings indicated that acceptable progress could be made in changing seed size in sorghum by using selection methods that would take advantage of the additive variance.

Eight R-lines and five A-lines, considered representative of the variability then available among grain sorghum lines, were used by Beil and Atkins (1967) to produce 40 F_1 hybrids for studies of combining ability. For 100-seed weight, they found significant amounts of variation for both GCA and SCA. The ratio for GCA/SCA of 3:1 indicated that additive gene action was more important than the nonadditive effects. In addition, interactions of general and specific effects with either locations or years gave very small and usually nonsignificant variance components. These findings indicated

that expression of seed weight among these hybrids was controlled primarily by the additive effects of genes that are stable over years and environments, and they provided support for the conclusions of Kambal and Webster (1965).

Beil and Atkins also indicated that seed size did not contribute as much to grain yield as did the number of seeds/panicle. Highest yields were obtained from plants that had one large head with many seeds. In contrast, Kirby and Atkins (1968) evaluated a similar set of 24 sorghum hybrids and found that SCA effects for seed size were highly significant ($P< 0.01$), whereas GCA effects were not significant.

Liang (1967) grew the F_1 hybrids from a diallel cross of six adapted sorghum varieties and found that GCA effects for seed size were not significant, but SCA effects exceeded the 0.01 probability level. However, the GCA/SCA ratio was 2:1, indicating that additive effects had a proportionately greater impact on seed size inheritance in these hybrids. Similarly, Chiang and Smith (1967) evaluated seed size of F_1 sorghum hybrids from a seven-parent diallel and found strong nonallelic interactions, measured as deviations from an additive model with complete dominance.

Eight R-lines developed from African introductions were crossed to four adapted A-lines to produce sorghum hybrids that were studied by Malm (1968). Results from a two-year experiment showed that the ratio of GCA:SCA effects was 64:1.

He concluded that, with these exotic materials, additive gene action was largely responsible for the expression of seed size, and that sorghum breeders, using similar materials, should be able to make significant progress in grain yield by selecting for seed size.

Laosuwan and Atkins (1977) estimated combining ability and heterosis in single crosses and three-way hybrids that were constituted by using 11 exotic lines from the sorghum conversion project as male parents (R-lines) and three adapted female parents (A-lines), Combine Kafir 60, KS24, and Martin. The 11 R-lines also were crossed to three male-sterile single crosses to produce three-way hybrids. For 100-seed weight, they found that GCA effects in the single crosses were highly significant and large compared to the nonsignificant SCA effects. In the three-way hybrids, only the GCA effects for males were significant ($P<0.01$). The GCA/SCA ratio for single crosses was 32:1 and for the three-way hybrids, it was 16:1. For both the single crosses and three-way hybrids, additive effects seemed most important in the inheritance of seed size.

Liang and Walter (1968) estimated gene effects in three sorghum crosses that had narrow-genetic bases, i.e., Redlan x Martin, Redlan x Combine 7078, and Plainsman x KS7. They found that additive effects played a minor role in the inheritance of 1000-seed weight, whereas dominance effects played a much larger role. Also, the additive x additive

and dominance x dominance effects made an appreciable contribution to the inheritance of 1000-seed weight. Heritability estimates for seed size ranged from 24 to 33%.

Fanous et al. (1971) calculated heritability values and expected genetic gain from selection for seed size by using data from five sorghum crosses: Woodward Big Head (WBH) x Chicken Maize (CM), OK24 x CM, Red Kafir CI34 x CM, OK24 x WBH, and OK8 x WBH. Heritabilities were estimated by using both the regression and variance-component methods. The average value for the individual plant regression method was 23%, and for the variance-component method, it was 81%. They concluded that progress from selection for increased seed size would be slow if selection was based on data from individual plants. They suggested further that selection for 100-seed weight possibly could be more effective among later generation progeny.

Although the estimates from the nine studies reviewed were derived from narrow-base germplasm, and the results are valid only for the sorghum lines used in each experiment, several general conclusions can be drawn. It seems clear that when materials with a large amount of exotic germplasm were used or when the parents showed large differences in seed size, the ratio of GCA:SCA was large. If narrow-base germplasm similar in seed size was used, the GCA/SCA estimates were much lower. It seems that, as the germplasm involved

becomes more adapted, a greater proportion of the additive effects become fixed and the variability that is expressed is largely a result of nonadditive gene effects.

Investigations with Wide-Base Populations

With the advent of male sterility, random-mating populations were developed and variance estimates were derived by several sorghum breeders from these wide-based germplasm pools. Ross et al. (1976) compared the performance of five sorghum random-mating populations (NP1BR, NP2B, NP3R, NP5R, and NP7BR) with each other and with two check hybrids (RS626 and RS671). They concluded that little genetic variability for grain yield and its components existed in NP1BR and NP2B and that little progress from selection could be expected. Grain yield and 1000-kernel weight data in NP7BR were biased because extremely low yielding panicles with small seeds were obtained from pollinated antherless (alal) male-sterile plants. Even with adjustments for the effects of the alal plants, NP7BR displayed relatively low yields and little variability. NP3R and NP5R, however, displayed considerable within-population variability for grain yield and its primary components and they concluded that population improvement schemes could be used successfully for these traits.

The performance of NP3R sorghum population was examined in more detail by Jan-Orn et al. (1976). Nine traits were

measured on 196 half-sib, 196 full-sib, and 196 S_1 families. Mean 1000-seed weights of full-sib and half-sib families were similar to those of S_1 families, indicating that heterosis and inbreeding depression were not of marked importance in this population for this trait. Estimates of additive genetic variance determined from both S_1 families and half-sib families tended to be inconsistent for most traits, including 1000-seed weight. They postulated that, in the S_1 families, dominance with frequencies of favorable alleles less than 0.5 and, in the half-sib families, nonrandom pollination of male-sterile plants could influence the estimates. The additive to dominance variance ratio for 1000-kernel weight was 12:1, indicating that the additive effects were considerably more important than dominance effects. The estimate of heritability for 1000-kernel weight was moderately high, 0.45, on an individual-plant basis. Estimates of response to selection for 1000-kernel weight by using different breeding systems showed that mass selection produced a gain of 14.6% per year. The gain was attributed largely to high heritability of the trait. However, they suggested that S_1 family testing would be most effective for yield and yield components, and that mass selection should be used only for highly heritable traits such as days to midbloom and plant height. They also concluded that most of the variation for grain yield in the NP3R population should be attributed to the number and not the

size of the kernels.

Eckebil et al. (1977) used the data from 200 S_1 families of three sorghum populations, NP3R, NP5R, and NP7BR, to obtain estimates of heritability and predicted gains from selection. Means of the three populations differed significantly for all traits except 1000-kernel weight. Genetic variances for seed size were greatest for NP5R, probably due to the contribution of large-seeded exotic lines to that population. Heritability estimates for seed size, on a progeny-mean basis, ranged from 0.86 to 0.91 for the three populations. Correlated responses to selection among the different traits also were examined. When selection was for 1000-kernel weight, grain yield increases were 49, 52, and 29% of the gain that would be expected if selection was directly for grain yield in NP3R, NP5R, and NP7BR, respectively.

Recurrent mass selection was used to improve grain yield in two random-mating sorghum populations by Obilana and El-Rouby (1980). After three cycles of selection for individual-plant yields, increases of 38 and 40% for grain yield were observed for two different composites. The rapid gain could be explained by the highly diverse nature of the population.

Bittinger et al. (1981) examined several quantitative traits in the PP9 sorghum population by using 90 randomly chosen half-sib families in a Design I experiment. The

additive to dominance variance was 2:1 for 100-seed weight. They concluded that reasonable genetic gain could be expected for major economic traits (e.g., grain yield) when broad-based sorghum populations are subjected to recurrent selection.

Lothrop (1983) compared the performance of 101 S_1 and 102 half-sib families from the sorghum population IAP1R in three environments. He found highly significant differences among the S_1 and half-sib families for 100-seed weight. Environment by half-sib and environment by S_1 family interactions were not significant, indicating that 100-seed weight was stable over environments. Heritability estimates for 100-seed weight, on a progeny-mean basis, were 0.74 and 0.82 for half-sib and S_1 families, respectively. On an individual-plant basis, the heritability estimate was 0.41 for 100-seed weight. He concluded that mass selection would be an excellent method for increasing seed size in this population. In a second experiment, Lothrop tested 119 S_1 lines from the same population in four environments. As before, there was highly significant variation among the S_1s for 100-seed weight, but the genotype by environment component also was significant. Seed weights ranged from 1.87 to 3.36 g per 100 seeds. Heritabilities calculated on a progeny-mean and on an individual-plot basis for 100-seed weight were 0.78 and 0.34, respectively. Heritability on an individual-plant basis was 0.43. Based on estimated gains per year, gridded mass selection was the best

method for increasing seed size, but S_1 family testing was superior for increasing grain yield, panicles/plant, and seeds/panicle.

Factors Affecting Seed Size in Sorghum

In the development of the sorghum seed, many related traits may affect the size of the seed. Beil and Atkins (1967) found nonsignificant positive correlations for grain yield and 100-seed weight among the parents, but there were significant positive correlations between these characters among 40 F_1 hybrids produced from these parents. Kirby and Atkins (1968) reported that five vegetative-plant characteristics, as well as grain yield, were positively correlated with 100-seed weight. A highly significant positive correlation was found between plant height and 100-seed weight, and negative but nonsignificant correlations were observed for 100-seed weight with seeds/panicle, panicles/plant, days to mid-bloom, number of leaves, and stem diameter. The correlation of 100-seed weight and grain yield among hybrids that involved exotic germplasm was moderately large ($r=0.52$) and highly significant ($P<0.01$) in studies reported by Malm (1968).

Niehaus and Pickett (1966) determined correlations among the hybrids from an eight-inbred diallel cross and found significant positive correlations for seed size with grain yield and seed size with plant height. There was essentially no

correlation between seed size and seeds/panicle and only a small positive correlation between panicles/plant and seed size. However, Liang et al. (1972) found negative correlations between grain yield and 100-seed weight in their experiment with 10 genotype-sets consisting of two pure lines, their F_1s, F_2s, and first backcrosses. Liang et al. (1969) also tested F_3 and F_4 lines from the crosses, Redlan x Martin and CK-60 x KS7, and did not find significant correlation between seed size and grain yield. They did find significant negative correlations of seed size with seeds/panicle and panicles/plant and hypothesized that these associations arose because of developmentally induced relationships.

Quinby and Schertz (1970) noted that an inverse relationship generally exists between seeds/panicle and seed size, and that selection for both traits concurrently would make progress in the improvement of grain yield slow or nonexistent. From tests of nine hybrids and their 18 parents, Blum (1970) found that seed size and seeds/panicle were negatively associated and that the strength of the association depended on the magnitude of expression for each trait.

Jan-Orn et al. (1976) calculated phenotypic correlations among several traits by using data from the sorghum population NP3BR. They found significant negative correlations ($P<0.01$) for seed size with days to midbloom and seeds/panicle for half-sib, full-sib, and S_1 families. In addition,

they found significant positive correlations ($P<0.01$) for plant height with seed size. Correlations for grain yield with seed size were small and their sign differed among family types. Highly significant positive correlations were observed for seed size and panicles/plant among the half-sib families, whereas correlations were positive and negative for full-sib and S_1 families, respectively, and not significant.

Eckebil et al. (1977) derived genetic correlations among eight agronomic traits using the data from 200 S_1 families from three populations, NP3R, NP5R, and NP7BR. They found positive correlations between seed size and plant height, with coefficients of 0.60, 0.52, and 0.33 for NP3R, NP5R, and NP7BR, respectively. Negative correlations were observed between seed size and days to midbloom, -0.39, -0.46, and -0.29, for NP3R, NP5R, and NP7BR, respectively. The correlations calculated for grain yield and seed size were 0.46, 0.52, and 0.28 and those for panicles/plant with seed size were 0.19, 0.42, and 0.08, for NP3R, NP5R, and NP7BR, respectively. Phenotypic correlations were determined from half-sib families of PP9 by Bittinger et al. (1981). They obtained values of 0.08 for yield and seed size, 0.49 for plant height with seed size, and -0.06 for days to midbloom and seed size.

Lothrop (1983) examined phenotypic and genetic correlations among yield traits measured on 101 S_1 and 102 half-sib

families from the third cycle of IAP1R. He found small but significant ($P<0.01$) phenotypic correlations for 100-seed weight and grain yield ($r=0.18$), 100-seed weight with panicles/plant ($r=0.15$), and a significant ($P<0.01$) negative correlation for 100-seed weight with seeds/panicle ($r=-0.58$) among the S_1 families. Similar phenotypic correlations were found among half-sib families in the same experiment. In a second experiment that involved 119 S_1 families, the correlation for 100-seed weight with grain yield was small but highly significant ($r=0.11$), the correlation of 100-seed weight with seeds/panicle was much higher ($r=-0.58$), while a nonsignificant negative correlation was recorded for 100-seed weight with panicles/plant ($r=-0.05$). The genotypic correlations for all characters in both experiments were similar in magnitude and direction to the phenotypic correlations.

Ross and Hookstra (1983) evaluated the performance of NP16BR by using data from 200 S_1 families grown in three different years. Correlations for seed size with grain yield and seeds/panicle were not consistent over years. However, heritability estimates for seed size were stable, with values of 0.77, 0.79, and 0.76, respectively, for the three years.

The specific character most often studied in relation to grain yield in sorghum is plant height. Casady (1965) investigated the effects of a single height gene ($\underline{Dw}_3$) on grain yield and its primary components. Presence of the $\underline{Dw}_3$ allele

resulted in higher grain yield, more panicles/plant, higher test weight, and higher 1000-seed weight than the $\underline{dw_3}\underline{dw_3}$ counterparts of Martin, Plainsman, and Redlan varieties. Effects of the same height gene ($\underline{Dw_3}$) also were evaluated by Campbell and Casady (1969). They found that the taller plants ($\underline{Dw_3}$-) always had significantly heavier 1000-seed weights. Graham and Lessman (1966) reported on a similar study that involved segregation at the $\underline{Dw_2}$ locus and found significant differences between the $\underline{Dw_2}$- and $\underline{dw_2}\underline{dw_2}$ genotypes. The $\underline{Dw_2}$- genotypes had higher grain yields and increased 100-seed weights. They concluded, however, that these advantages may or may not be due to differences in plant height or leaf area, but rather to other factors such as light interception potential or spatial arrangement of the leaves.

A summary of the grain sorghum literature concerning seed size indicates that, although there is a lack of diversity for this trait among hybrids and inbreds currently in production, large amounts of variability for improving seed size are available within the genus Sorghum. Recurrent selection has been effective in improving characters such as grain yield, and disease and insect resistance in grain sorghum populations. Gridded mass selection for 100-seed weight improvement should also be effective because seed

weight (1) is controlled primarily by additive gene effects, (2) exhibits high individual-plant heritability, and (3) demonstrates small genotype by environment interaction. Difficulties in improving 100-seed weight in combine-height grain sorghums could be encountered due to strong positive correlations with plant height. Indirect gains in grain yield also may be difficult to obtain because of compensatory effects of the yield components seeds/panicle and panicles/plant when 100-seed weight is undergoing direct selection.

Seed Size Studies in Other Crops

The use of seed size, or weight per unit, for species improvement has been attempted in many crops. Reasons for the interest in seed size differ among species, but usually they relate to traits such as emergence of seedlings, stand establishment, biological yield, or to specific seed quality or processing traits.

Ford (1965) conducted studies with flax (Linum usitatismum L.) and found that large-seeded types had no advantage in seed yield and were more sensitive to environmental stress. Small-seeded types compensated for environmental stresses by producing more seeds/boll and developing

more bolls, which resulted in higher yields. In studies with safflower (Carthamus tinctorius L.), Kotecha and Zimmerman (1978) found that the variability in seed size was largely genetic in nature with no maternal or nonadditive gene effects expressed. Heritability values of 0.50 and 0.90 were calculated from experiments conducted in two different years, indicating that environmental effects could strongly influence the heritability of seed size.

Size of the seed in sunflower (Helianthus annus) has received considerable study in relation to oil yield. Putt (1943), Russell (1953), and Fick et al. (1974) all found negative correlations between seed size and oil content among different groups of inbreds. However, Fick et al. (1974) did not find this relationship among open-pollinated and hybrid varieties. Beard and Geng (1982) found a correlation of 0.32 for seed size and grain yield, indicating that selection for seed size should result in some increase in grain yield in sunflower. Genetic effects were estimated for several characters in sunflower by Miller et al. (1980) from hybrids obtained by crossing two pollinator inbreds to 10 randomly chosen female parents. They found that seed size was controlled primarily by additive gene effects, and suggested that breeding schemes which capitalize on the large

additive portions of the genetic variance should be used for population improvement.

In crosses of Vicia sativa x V. angustifolia, Allen and Donnelly (1965) found that seed of intermediate size had the fastest field emergence. Hsu (1979) studied seed size in common bean (Phaseolus vulgaris L.) and found that both the embryo and seed coat contributed to the final size of the seed, with the embryo being the major determinant. He found that two processes occur during seed development: (1) formation of cellular structure and (2) filling the cells with storage material, and concluded that the second may be more important in determining final size of the seed in common bean. Sinnott (1921) found that plant size of red kidney bean (Phaseolus vulgaris L.) was correlated with organ size, but only to a certain plant size. After that size is achieved, a further increase in plant size did not result in an increase in organ size. He hypothesized that the size of an organ is not actually correlated with plant size, but with size of the axial growing point from which the organ develops.

Brim and Cockerham (1961) found additive gene action the principal component of genetic variance for seed size in populations from crosses of N48-4860 x Lee and Roanoke x Lee soybeans (Glycine max (L.) Merrill). Anand and Torrie (1963) determined that seed size was highly heritable in soybeans, but it was not correlated (r=0.33, -0.03, -0.07) with seed

yield in their experiments with progeny from three crosses. Fehr and Weber (1968), using mass selection for specific gravity and size of the seed, increased protein content and decreased oil percentage in soybean populations. They obtained greatest progress for high protein and low oil percentage when selection was for large seed and also noted that a linear change in seed size was attained with each cycle of selection. Johnson et al. (1955) found that only a small percentage of the variability for seed size in two soybean populations was environmental, that heritabilities were high in both populations (0.68 and 0.92), and that good gains in seed size could be made from direct selection.

Nguyen and Sleper (1983) investigated the nature of genetic variability in tall fescue (Festuca arundinacea Schreb.). Additive gene action accounted for most of the genetic variance for 100-seed weight. Because of the high genotypic correlation (r=0.98) between maturity and 100-seed weight, they believed that indirect selection would be advantageous for increasing 100-seed weight because maturity could be recorded easily. In turn, the selection should produce higher yields due to the high phenotypic correlation (r=0.67) between seed yield and 100-seed weight. Trupp and Carlson (1971) improved seedling vigor in smooth bromegrass (Bromis inermis Leyss.) by using recurrent selection for large seed. In five native grass species, Kneebone and Cremer (1955) found

that seed size had little effect on germination, but genotypes with large seed produced more vigorous seedlings and exhibited faster rates of emergence and plant growth than the small-seeded types.

Stand establishment is an important cultural consideration in many forage legumes. Cope (1966) found that seed size in Sericea lespedeza (Lespedeza cuneata Dumont) was correlated significantly with seedling height and weight (r=0.74 and 0.76, respectively). He believed that selection for seed size would involve genetic factors for growth rate as well as for seed size. Birdsfoot trefoil (Lotus corniculatus L.) seedlings from large seeds were significantly more productive and had the ability to produce basal shoots at an earlier age than seedlings from small seeds in the experiments of Henson and Tayman (1961). Fransen and Cooper (1976) found seed size the dominant factor affecting seedling growth in sainfoin (Onobrychis viciifoila Seop.). They hypothesized that the larger leaf primordia and embryo associated with large seeds may reflect a more advanced stage of embryo development and may be more important in the attainment of rapid germination and emergence than large food reserves in the cotyledons. However, Carleton and Cooper (1972) found that differences in seed size may be correlated with seedling weight in some species (e.g., birdsfoot trefoil, r=0.89) but not others (alfalfa, Medicago sativa, r = 0.21) and sainfoin

(r=0.59). It seems that in many forage species, an increase in seed size will provide for an increase in seedling survival and, in turn, for better stands and improved yields.

In small grains, seed size has been used both directly and indirectly to improve grain yields. Rasmusson and Cannel (1970) hypothesized that selection for large kernels in barley (Hordeum vulgare L.) would be advantageous in all environments because it is the last yield component to be developed and its level of expression should not produce compensatory effects in other components. Because seed size is finalized during the last step before physiological maturity, there is little reason for the plant to conserve nutrients or water at that time. However, they observed that selection for 100-kernel weight as a means to improve yield was effective in one barley population but not in another. They concluded, therefore, that selection for yield via 100-kernel weight may be effective in specific situations, but they would not recommend it as a standard practice. Yap and Harvey (1972) used F_1 lines from a seven-cultivar diallel cross to investigate genetic variance in barley. Their results showed that both additive and dominance effects were important in the determination of kernel size. Barley seedlings from large seeds, tested by McDaniel (1969), had a greater quantity of mitochondrial protein than those from small seeds. He proposed that there was a higher respiration rate and more ATP

production in the large-seeded types, resulting in a greater growth potential.

Frey (1962) evaluated the inheritance of seed size and its relation to grain yield in F_2-derived lines from eight oat (Avena sativa L.) crosses. He concluded that seed size was of little value in selecting indirectly for grain yield, and that selecting for grain yield plus seed size concurrently decreased the gain for grain yield. However, Khadr and Frey (1965) evaluated progress from recurrent selection for 100-seed weight in oats and found that realized genetic advance and predicted advances were very close. They also found that improved populations maintained their variability for seed size and other unselected traits over cycles. Frey and Huang (1969) pointed out the importance of having a large range in the size of seed in populations evaluated for interrelationships with other traits. With small ranges in seed size, correlations between grain yield and seed size could be either positive, negative, or zero. They concluded that selection for seed size may be a valuable way to improve grain yield in oats, in contrast to the recommendations of an earlier paper by Frey (1962). Hathcock and McDaniel (1973) found no expression of heterosis for 1000-kernel weight in the F_1 and F_2 progeny of crosses among 10 pure-line oat cultivars.

Peterson et al. (1982) found that kernel weight (mg) was not correlated with number or size of vascular bundles, phloem

areas, or sieve tube members in oats. The number and size of vascular bundles seemed to develop in concordance with the number of spikelets initiated. They concluded that, at the upper stem internode, the area available for transport does not restrict grain filling but restrictions may occur elsewhere, such as in the floret or rachilla.

Wheat (Triticum aestivum L.) has been studied extensively in relation to using increased seed size as a method of improving grain yields. Sharma and Knott (1964) used parental F_1, F_1-backcross, F_2, and F_2-backcross plants, and F_3 lines of a cross between Chagot and Selkirk spring wheat to study the inheritance of seed size. They determined that as few as four genes control seed size, that it is highly heritable, and that additive genetic variance was a sizable part of the total genetic variance. Baker et al. (1968) used 50 random lines in the F_7 generation from the cross of CT423 x Prelude to demonstrate that 1000-kernel weight and grain yield were correlated ($r=0.33$). Fonseca and Patterson (1968) used F_1 and F_2 generation progenies from a seven-parent diallel cross of winter wheat to show that the number of spikes, 100-kernel weight, and number of kernels/spike were all significantly correlated with grain yield ($r=0.71$, 0.40, and 0.18, respectively). Each trait had a direct effect on grain yield, and there were important indirect effects as well, due to negative correlations among the yield components.

Lebsock and Amaya (1969) found that tallness and late maturity were associated with large kernels in durum wheat (Triticum durum); but it appeared that selection of short, early large-kernel types was possible. Their data also showed that kernel size might be used for rapid indirect selection for high test weight and possibly for grain yield in F_2 and F_3 populations. Knott and Talukdar (1971) transferred high 1000-kernel weight from Selkirk to Thatcher and found that grain yields in wheat tend to be stabilized by compensation among the grain yield components. They observed, however, that the compensation is not always complete and that selection among the components may result in increased grain yields.

Data from the F_1, F_2, backcross-F_1, and parental lines of a four-cultivar spring wheat diallel cross were examined by Sun et al. (1972). They found that a large amount of the genetic variance for kernel size was additive and that standard pedigree selection schemes should be useful for developing lines with a desired kernel size. Bhatt (1972) also studied seed size in spring wheat, and determined that gene action was primarily additive. McVetty and Evans (1980) found in a combined-cross analysis of three spring wheat crosses with a common female parent that 1000-kernel weight of F_2 plants was not correlated with grain yields of F_4 bulk populations. Sharma et al. (1981) reported that differences among correlations for seed size with protein percentage were

highly dependent on the Triticum species tested.

Ledent (1982) examined the performance of 33 genotypes of winter wheat over a four-year period and found no yield component which consistently accounted for the differences in grain yield among cultivars. Busch and Kofoid (1982) used recurrent selection for kernel weight in spring wheat and reported a 3% gain/cycle, based on the evaluation of 80 random S_4 and S_5 lines from the C0 and C2. They estimated a 7% gain/cycle based on tests with bulks of the C1 through C4. Two cycles of selection produced lines with higher 1000-kernel weights than any in the C0. They concluded that recurrent selection should be effective in spring wheat for the improvement of specific traits.

Gebeyehou et al. (1982) reported that duration of grain filling and duration of vegetative growth both had marked influence on 250-kernel weight of wheat. The winter wheat germplasm-line Benni was used by Ibrahim et al. (1983) in crosses with Sullivan and Sava. Analyses of F_3 families plus parental, F_1, F_1-backcross, and F_2 populations showed nonsignificant genotypic correlations between kernels/spikelet and 200-kernel weight and they suggested there should be little difficulty in improving both traits simultaneously.

Maize breeders, using yield component selection, tend to use traits other than kernel weight per unit as the character of selection (Laible and Dirks, 1968; Geadelmann and Peterson,

1978; Cortez-Mendoza and Hallauer, 1979). Leng (1963) found that heterotic effects for 100-kernel weight were small and that heritability of the primary yield components (ears/plant, ear length, kernel depth, and row number) was much higher than the heritability of 100-kernel weight. He observed that the highest yields in maize tended to be associated with F_1 hybrids that had medium to medium-high 100-kernel weights. Johnson and Tanner (1972) determined the leaf area index (LAI) and percentage light penetration (LP) for the double cross United-10, its two parental single crosses, and their respective inbred parents. They found at equal LAI and LP that differences in grain yield among the maize inbreds and hybrids were closely associated with differences in 100-kernel weight.

Jones and Simmons (1983) found that rate and duration of growth and final 50-kernel weights in maize were not increased significantly in response to treatments that increased available photosynthates. They concluded this may be due to (1) late increases in carbohydrate supply, (2) factors other than carbohydrate supply limit the growth rate, and (3) final seed size and kernel growth rates may already be at a genetic limit in the hybrid studied. Bell et al. (1983) used 11 cycles of recurrent selection for increased seedling emergence and heavy seed weight per unit in a sh2 maize population. Significant differences for test weight were observed among

cycles but grain yield showed no change. The authors suggest that, since no visual differences were observed between cycles for seed size or shape, selection resulted in kernels with significantly more nutrient reserve while retaining the sh2 characteristics.

Previous studies indicate that the reasons for improving 100-seed weight differ according to the specific crop. In oil crops, such as flax, sunflower, and soybean, large seed generally is associated with low oil yields. However, large seed is important for improving protein content in soybeans. In the studies reviewed, selection for increased seed size in forage legumes and grasses commonly resulted in larger seed, which generally produced more vigorous seedlings. Increased seed size did not influence grain yield directly, but it led to improved stand establishment in most species. In the small grains (oat, barley, and wheat), selection for increased 100-seed weight generally resulted in small increases in grain yield. Compensation among yield components, however, resulted in gains less than expected when direct selection for grain yield was practiced. Finally, in maize, indirect selection for 100-seed weight has not been used for improving grain yield because other yield components tend to produce better indirect gains in yield. However, selection for heavy 100-seed weight in maize has been used for the specific application of improving seedling emergence in a shrunken endosperm (sh_2) population.

MATERIALS AND METHODS

Development of IAP3BR(M)

Iowa population 3 is a random mating grain sorghum population that has been advanced through four cycles of gridded mass selection for large seed. It should serve as a potential source of both B-lines (fertility nonrestorer) and R-lines (fertility restorer), and is designated IAP3BR(M)C4 in accordance with sorghum population nomenclature as described by Atkins (1971). Development of the population was initiated in 1976 at Ames, Iowa, by R. E. Atkins (Atkins, 1982), who made controlled crosses of 30 lines onto bagged genetic male-sterile segregates ($\underline{ms_3}\underline{ms_3}$) from IAP1R(M)C1 random-mating population (Atkins, 1980). Many, but not all, of the 30 lines had been tested and established as pollen fertility restorers (R-lines) in the A_1 milo-kafir cytoplasmic-genetic-male-sterility system (Stephens and Holland, 1954). The 30 lines were chosen as the most desirable agronomic types from a collection of 116 large-seeded genotypes that were obtained from sorghum breeders in 10 states. Designations of the lines are given in Table 1. Equal amounts of seed from the 30 crosses were composited and, in 1977, a 600-g sample was planted near Ames in an isolation plot of 0.09 ha (0.23 A), which gave a population of approximately 6000 plants. The isolation block was made up of 30

Table 1. Sorghum lines that were crossed onto bagged genetic male-sterile segregates of IAP1R(M)C1 to initiate IAP3BR(M)

Designation	Designation
IS 2403C	Tx Bk-13
IS 3063C	Tx Bk-29
IS 3464C	Tx Bk-30
IS 3579C	NP73-2815
IS 7340C	NP73-2824
IS 7367C	RWD Y13
IS 7435C	IA 70-124
IS 7452C	NMR-13 Sel.
IS 7809C	NMR-16 Sel.
IS 10929	NMR-19 Sel.
IS 12635	NMR-24 Sel.
SC 0133-6-1	NM68-2576
TAM 30	NM68-2582
TAM 2553	NM, BTx3118xR4
TAM 2559	NM, BTx3118xR17

rows, 30.5 m (100 ft) long, spaced 100 cm (40 in.) apart. Thirty cells of a grid were superimposed on the isolation block, each cell being 5 rows wide by 6.1 m (20 ft) long. Panicles borne on the main culms of fertile plants were

tagged during anthesis. All plants in the C0 were fertile, with the genotype $\underline{Ms_3}\underline{ms_3}$. At harvest, 15-20 tagged fertile panicles of combine height (100-150 cm (40-60 in.)) were harvested from each cell in the grid. Seed development was hampered by an early autumn freeze that made 100-seed weights lighter than normal. A total of 491 fertile panicles were harvested, threshed individually, and 100-seed weights were taken. Ten panicles with the heaviest 100-seed weight from each of the 30 cells of the grid were composited to advance the population to the C1 in 1978.

The C1 isolation was planted near Ames in 1978 in the same manner as the C0 isolation. Male-sterile segregates ($\underline{ms_3}\underline{ms_3}$) appeared in the C1 planting. Different colored tags were secured around the peduncle at anthesis to identify male-sterile and fertile plants. At harvest, 15-25 agronomically desirable fertile and male-sterile plants were harvested from each cell in the grid. All panicles were threshed individually, and 100-seed weights were taken.

Seed for the C2 was obtained by making a composite of the 73 panicles with the heaviest 100-seed weight among the 485 male-sterile panicles harvested in 1978. Each cell of the grid was represented in this composite. Growing conditions were good at Ames in 1979, and 479 male-sterile and 388 fertile panicles were harvested from the C2 isolation planting. Procedures for the C3 isolation block in 1980 were similar to

those for previous cycles. Seeds from 74 panicles with the heaviest 100-seed weights among the 479 male-sterile panicles harvested in the C2 were composited, with each cell of the C2 isolation represented. Similarly, a composite of 64 panicles with the heaviest 100-seed weights among the 429 male-sterile panicles harvested in the C3 were used to plant the C4 isolation block (additionally, 414 fertile panicles were harvested from the C3). A total of 437 male-sterile panicles and 422 fertile panicles were saved from the C4 isolation. The number of male-sterile panicles composited to advance the population in each cycle represented about 15% of the male-sterile panicles harvested from that isolation planting. Composites of seed from fertile and male-sterile panicles harvested from the C3 were released to the public as IAP3BR(M)C3 in 1982.

Experimental Procedure

Seed for Experiment I and Experiment II came from isolation plantings of the different cycles of IAP3BR. Entries in Experiment I consisted of composites of seed from fertile panicles of the C0, C2, C3, and C4, and composites from male-sterile panicles of the C1, C2, C3, and C4, providing a total of 8 entries. Experiment II evaluated 120 S_1 lines (derived from fertile panicles), 60 lines chosen randomly from the C0 and C4. Both Experiment I and Experiment II were grown in

central Iowa (Ames), southern Iowa (Beaconsfield), and northwest Iowa (Sutherland) during 1982 and 1983.

Experiments I and II were planted in Clarion-Webster soil at Ames, in Shelby-Grundy soil at Beaconsfield, and in Galva-Primghar soil at Sutherland. Planting dates at Ames were June 1, 1982 and May 26, 1983; at Beaconsfield they were June 7, 1982 and June 1, 1983; and at Sutherland, planting dates were June 3, 1982 and May 23, 1983.

The experimental unit for both experiments was a 3.05 m (10 ft) section of a single-row plot 4.27 m (14 ft) long. The space between rows was 102 cm (40 in.). Both experiments were overplanted with the seed distributed through a funnel planter. When seedlings reached the 3-4 leaf stage, plots were thinned to approximately 8 cm between plants in 1982 and 10 cm in 1983. This resulted in populations of 129,275 plants/ha (52,275 plants/acre) in 1982 and 96,885 plants/ha (39,210 plants/acre) in 1983.

Soon after thinning, a 3 m (10 ft) section of competitive plants in each experimental unit was marked with a garden stake at each end and the number of plants in that section was recorded. This section of the experimental unit was harvested for grain yield determinations. When 3 m of competitive plants were not available, a shorter plot was marked and grain yields were adjusted arithmetically. In no case was the experimental unit less than 1.5 m (5 ft).

Data were recorded for days to midbloom and plant height in 1982 and 1983 only at Ames. A plant was considered at midbloom when florets were open and anthers extruded down to the middle of the panicle borne on the main culm. Plant height was measured on the main culms from the soil surface to the tip of the panicles, when plants were well into the grain-filling period.

An additional character, panicle type, was recorded for Experiment II at all locations in 1983. The scale was 1 = compact, 2 = semicompact, 3 = semiopen, and 4 = open. Data for days to midbloom and plant height in Experiments I and II and panicle type in Experiment II represent an average expression for those traits in each plot. Plant to plant expression of the traits was quite variable because of the segregating nature of the S_1 lines (families) and the composites (bulk populations).

Plots were harvested in October of each year when grain moisture content reached the 20-25% range. Panicles from the 3 m staked section of each plot were counted as they were severed just below the lowest panicle branch, placed in an Osnaburg (AM size) cloth bag, and dried artificially for three days at 70°C (160°F). After drying, the total weight (grain, pedicles, panicle branches) of each plot was recorded to the nearest 20th of a pound.

Grain yields were calculated in quintals per hectare

(q/ha) from the dry head weights, according to the regression method described by Robinson and Bernat (1963). Six plots with dry head weights above the mean and six plots with weights below the mean were selected randomly from each location in each year for Experiment II. These plots were threshed using an Almaco LPT All Purpose Plot Thresher and weights of the threshed grain for each plot were recorded. A regression equation was then developed by using the threshed grain weights (Y) and dry head weights (X):

Let $\bar{X}_a$ = mean of 6 entries with dry head weights above the mean of all entries.

$\bar{X}_b$ = mean of 6 entries with dry head weights below the mean of all entries.

$\bar{Y}_a$ = mean threshed grain weights of 6 entries above the mean of all entries for dry head weight x 14.64 (a factor to express grain yield on a q/ha basis).

$\bar{Y}_b$ = mean threshed grain weights of 6 entries below the mean of all entries for dry head weight x 14.64.

$\bar{X}$ = mean dry head weight of the 12 selected entries.

$\bar{Y}$ = mean threshed grain weight of the 12 selected entries.

$b = (\bar{Y}_a - \bar{Y}_b)/(\bar{X}_a - \bar{X}_b)$.

$a = \bar{Y} - b\bar{X}$

$Y = a + bX$ is the form of the completed regression equation.

The equations developed to convert lb/plot of dry panicles to q/ha of threshed grain were:

Ames, 1982	Y = 2.07 + 10.75X
Ames, 1983	Y = 9.96 + 10.57X
Beaconsfield, 1982	Y = -4.25 + 11.63X
Beaconsfield, 1983	Y = 1.25 + 11.63X
Sutherland, 1982	Y = -0.79 + 9.28X
Sutherland, 1983	Not harvested for grain yield

These equations were used to calculate grain yields for both Experiment I and Experiment II. Although the sampled plots were all from Experiment II, similar regression lines would be developed for Experiment I because all entries were derived from the same population. No regression equation was developed for Sutherland, 1983, because those plots were harvested for 100-seed weight only.

Seed size was determined in both experiments from a five-panicle sample, threshed in bulk, for each plot. One hundred whole kernels were taken from each sample and weighed to the nearest centrigram by using an electronic balance. The number of panicles per plant was determined from panicle counts (taken at harvest) divided by the stand counts (taken after thinning). Average number of seeds per panicle was determined by using the following formula:

$$\text{Seeds/panicle} = \frac{\text{Grain weight (in g/plot)}}{\text{Panicles/plot x 100-seed wt (g)}} \times 100$$

Statistical Procedure - Experiment I

A randomized complete-block design was used for Experiment I. The eight entries consisted of the seed composites from fertile heads of the C0, C2, C3, and C4, and the composites from male-sterile heads of the C1, C2, C3, and C4. The fertile heads represent S_1 families (or lines) and the male-sterile heads represent half-sib families. Four replicates were grown at three locations each year. Environments (year-location combinations) and replicates were considered random variables. Cycles and family types were considered fixed variables. The linear model for each environment analysis in Experiment I was:

$$Y_{jkm} = \mu + R_j + F_m + C_{k(m)} + e_{jk(m)} \quad ,$$

where $j = 1 \ldots r$ replications; $m = 1 \ldots f$ family types; $k = 1 \ldots c$ cycles; and Y_{jkm} = observed value for the k^{th} cycle within the m^{th} family type within the j^{th} replicate; μ = overall mean; R_j = effect of the j^{th} replicate; F_m = effect of the m^{th} family type; $C_{k(m)}$ = effect of the k^{th} cycle within the m^{th} family type; $e_{jk(m)}$ = experimental error.

The linear model for the combined environment analysis in Experiment I was:

$$Y_{ijkm} = \mu + E_i + R(Y)_{ij} + F_m + C_{k(m)} + YF_{im} + YC_{ik(m)} + e_{ijk(m)} \quad ,$$

where i = 1 ... y environments; j = 1 ... r replications; m = 1 ... f family types; k = 1 ... c cycles; and Y_{ijkm} = the observed value of the m^{th} family within the k^{th} cycle of the j^{th} replication and i^{th} environment; μ = overall mean; E_i = effect of the i^{th} environment; $R(Y)_{ij}$ = effect of the j^{th} replicate within the i^{th} environment; F_m = effect of the m^{th} family type; $C_{k(m)}$ = effect of the k^{th} cycle within the m^{th} family type; YF_{im} = effect of the interaction of the i^{th} environment within the m^{th} family type; $YC_{ik(m)}$ = effect of the interaction of the i^{th} environment within the k^{th} cycle within the m^{th} family type; $e_{ijk(m)}$ = experimental error.

The expected mean squares for Experiment I are shown in Table 2 for each environment and in Table 3 for the combined environment ANOVA.

Statistical Procedure - Experiment II

A sets within replicates field design was used for Experiment II. There were two replicates in each environment, with six sets containing both cycles (C0 and C4) in each replicate. Twenty genotypes (10 C0 and 10 C4) were planted in a randomized arrangement in each set. However, incomplete data for some genotypes caused some sets to have data from less than 20 genotypes for the variables grain yield, panicles/plant, and seeds/panicle. All effects, except those attributable to sets, were considered random. The linear

Table 2. Expected mean squares for Experiment I for each environment

Source of variation	df	Mean square	Expected mean squares	F test
Replications (rep)	3	MS1	$\sigma_e^2 + cf\sigma_r^2$	MS1/MS9
S_1 vs HS	1	MS2	$\sigma_e^2 + rc\Sigma F^2/(f-1)$	MS2/MS9
HS linear	1	MS3	$\sigma_e^2 + r\Sigma(C_{HSL})^2/(C-1)$	MS3/MS9
HS quadratic	1	MS4	$\sigma_e^2 + r\Sigma(C_{HSQ})^2/(C-1)$	MS4/MS9
HS cubic	1	MS5	$\sigma_e^2 + r\Sigma(C_{HSC})^2/(C-1)$	MS5/MS9
S_1 linear	1	MS6	$\sigma_e^2 + r\Sigma(C_{S1L})^2/(C-1)$	MS6/MS9
S_1 quadratic	1	MS7	$\sigma_e^2 + r\Sigma(C_{S1Q})^2/(C-1)$	MS7/MS9
S_1 cubic	1	MS8	$\sigma_e^2 + r\Sigma(C_{S1C})^2/(C-1)$	MS8/MS9
Error	21	MS9	σ_e^2	

Table 3. Expected mean squares for Experiment I in the combined-environment ANOVA

Source of variation	df	Mean square	Expected mean square	F test
Environments (env)	5	MS1	$\sigma_e^2 + cf\sigma_{R(Y)}^2 + rcf\sigma_Y^2$	MS1/MS2
Replications/env	18	MS2	$\sigma_e^2 + cf\sigma_{R(Y)}^2$	MS2/MS12
S_1 vs HS	1	MS3	$\sigma_e^2 + rc\sigma_{(F)(Y)}^2 + rcy\Sigma F^2/(f-1)$	MS3/MS10
HS linear	1	MS4	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{HSL})^2/(C-1)$	MS4/MS11
HS quadratic	1	MS5	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{HSQ})^2/(C-1)$	MS5/MS11
HS cubic	1	MS6	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{HSC})^2/(C-1)$	MS6/MS11
S_1 linear	1	MS7	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{S1L})^2/(C-1)$	MS7/MS11
S_1 quadratic	1	MS8	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{S1Q})^2/(C-1)$	MS8/MS11
S_1 cubic	1	MS9	$\sigma_e^2 + r\sigma_{C(F)Y}^2 + ry\Sigma(C_{S1C})^2/(C-1)$	MS9/MS11
S_1 vs HS x env	5	MS10	$\sigma_e^2 + rc\sigma_{(F)Y}^2$	MS10/MS12
Cycles within S_1 and HS x env	30	MS11	$\sigma_e^2 + r\sigma_{C(F)Y}^2$	MS11/MS12
Error	126	MS12	σ_e^2	

model for each environments analysis in Experiment II was:

$$Y_{ijkm} = \mu + R_i + S_{j(i)} + C_k + L_{m(kj)} + e_{ijkm} ,$$

where i = 1 ... r replications; j = 1 ... s sets; k = 1 ... c cycles; m = 1 ... l genotypes for each cycle; and Y_{ijkm} = observed value for the m^{th} genotype in the k^{th} cycle and the j^{th} set of the i^{th} replicate; μ = overall mean; R_i = effect of the i^{th} replicate; $S_{j(i)}$ = effect of the j^{th} set within the i^{th} replicate; C_k = effect of the k^{th} cycle; $L_{m(kj)}$ = effect of the m^{th} genotype within the k^{th} cycle and j^{th} set; and e_{ijkm} = experimental error.

The linear model for the combined-environment analyses in Experiment II was:

$$Y_{hijkm} = \mu + N_h + R(N)_{i(h)} + S(R)_{j(i)} + C_k + L_{m(kj)} + NL_{hm(kj)} + NC_{hk} + NS(R)_{hj(i)} + e_{hijkm} ,$$

where h = 1 ... n environments; i = 1 ... r replications; j = 1 ... s sets; k = 1 ... c cycles; m = 1 ... ℓ genotypes for each cycle; and Y_{hijkm} = observed value for the m^{th} genotype of the k^{th} cycle within the j^{th} set and i^{th} replicate in the h^{th} environment; where μ = overall mean; N_h = effect of the h^{th} environment; $R(N)_{i(h)}$ = effect of the i^{th} replicate within the h^{th} environment; $S(R)_{j(i)}$ = effect of the j^{th} set within the i^{th} replicate; C_k = effect of the k^{th} cycle; $L_{m(kj)}$ = effect of the m^{th} line within the k^{th} cycle and j^{th} set; $NL_{m(kj)h}$ = effect of the interaction of the h^{th} environ-

ment within the m^{th} genotype nested within the j^{th} set and k^{th} cycle; NC_{hk} = effect of the interaction of the h^{th} environment within the k^{th} cycle; $NS(R)_{hj(i)}$ = effect of the interaction of the h^{th} environment within the j^{th} set within the i^{th} replicate; e_{hijkm} = experimental error.

The expected mean squares for Experiment II are presented in Table 4 for the single environment and in Table 5 for the combined analyses.

Data Analyses

The field and laboratory data collected from Experiments I and II were transferred to disk files and analyzed by using the facilities of the Iowa State University Computation Center, Ames, Iowa. Analyses were calculated on individual-plot data by using the PROC ANOVA, PROC GLM, and PROC MEANS options of SAS82 and the PROC ANOVA options of SAS72 (Statistical Analysis System, The SAS Institute Inc., Cary North Carolina). Data from Experiment I are presented in Table 6 through 9 and include mean squares from the analyses of variance, means for entries according to specific groupings, and estimates of total inbreeding depression.

Inbreeding depression was estimated by using data from the S_1 and half-sib families tested in Experiment I. An estimate of total inbreeding depression that would occur was calculated by using the following formula:

Table 4. Form of the ANOVA and expected mean squares for Experiment II in a single environment

Source of variation	df	Mean square	Expected mean squares	F test
Replications (rep)	r-1	MS1	$\sigma_e^2 + cls\sigma_R^2$	MS1/MS10
Sets/rep	r(s-1)	MS2	$\sigma_e^2 + clr\Sigma(S)^2/(S-1)$	MS2/MS10
Genotypes/sets	s(cm-1)	MS3	$\sigma_e^2 + r\sigma_{G(S)}^2$	MS3/MS10
C0 vs C4/sets	s(c-1)	MS4	$\sigma_1^2 + r\sigma_{C0C4(S)}^2$	MS4/MS7
C0/sets	s(m-1)	MS5	$\sigma_2^2 + r\sigma_{C0(S)}^2$	MS5/MS8
C4/sets	s(m-1)	MS6	$\sigma_3^2 + r\sigma_{C4(S)}^2$	MS6/MS9
C0 vs C4 error	s(c-1)	MS7	σ_1^2	
C0 error	s(m-1)	MS8	σ_2^2	
C4 error	s(m-1)	MS9	σ_3^2	
Error	s(cm-1)	MS10	σ_e^2	

Table 5. Form of the ANOVA and expected mean squares for the combined analyses of Experiment II

Source of variation	df	Mean square
Environments (env)	n-1	MS1
Replications (rep)/env	r-1	MS2
Sets/rep	r(s-1)	MS3
Genotypes/sets	s(cm-1)	MS4
C0 vs C4/sets	s(c-1)	MS5
C0/sets	s(m-1)	MS6
C4/sets	s(m-1)	MS7
(Sets/rep) x env	r(s-1)(n-1)	MS8
(Genotype/sets) x env	s(cm-1)(n-1)	MS9
C0 vs C4/sets x env	s(c-1)(n-1)	MS10
C0/sets x env	s(m-1)(n-1)	MS11
C4/sets x env	s(m-1)(n-1)	MS12
C0 vs C4 error	ns(c-1)	MS13
C0 error	ns(m-1)	MS14
C4 error	ns(m-1)	MS15
Error	ns(cm-1)	MS16

Expected mean squares	F test
$\sigma_e^2 + cls\sigma_{R(E)}^2 + clsr\sigma_E^2$	MS1/MS2
$\sigma_e^2 + cls\sigma_{R(E)}^2$	MS2/MS16
$\sigma_e^2 + cl\sigma_{S(R)E}^2 + rncl\Sigma(S)^2/(s-1)$	MS3/MS8
$\sigma_e^2 + cl\sigma_{S(R)E}^2 + rn\sigma_{g(s)}^2$	MS4/MS9
$\sigma_1^2 + rl\sigma_{COC4(S)E}^2 + rln\Sigma(COC4(S))^2/((COC4(S))-1)$	MS5/MS10
$\sigma_2^2 + r\sigma_{CO(S)E}^2 + rn\sigma_{CO(S)}^2$	MS6/MS11
$\sigma_3^2 + r\sigma_{C4(S)E}^2 + rn\sigma_{C4(S)}^2$	MS7/MS12
$\sigma_e^2 + cl\sigma_{S(R)E}^2$	MS8/MS16
$\sigma_e^2 + r\sigma_{G(S)E}^2$	MS9/MS16
$\sigma_1^2 + rl\sigma_{COC4(S)E}^2$	MS10/MS13
$\sigma_2^2 + r\sigma_{CO(S)E}^2$	MS11/MS14
$\sigma_3^2 + r\sigma_{C4(S)E}^2$	MS12/MS15
σ_1^2	
σ_2^2	
σ_3^2	
σ_e^2	

$$\frac{\bar{X}_{S_1} - \bar{X}_{HS}}{\bar{X}_{HS}} \times 200 \quad ,$$

where $\bar{X}_{S_1}$ = mean of S_1 families and $\bar{X}_{HS}$ = mean of half-sib families. Because the half-sib families were derived from male-sterile panicles that were pollinated randomly, they were considered noninbred with F = 0. In contrast, S_1 families were descendant from fertile panicles that were predominantly self-pollinated and thus inbred one generation, with F = ½. Because homozygosity will increase at the rate of 50% each selfed generation, the difference in means between S_1 and HS families for a given character should estimate one-half of the total inbreeding depression that would occur.

Data from Experiment II are presented in Tables 10 through 18 and include mean squares from the analyses of variance, cycle means, high and low genotype means, variance-component estimates, heritability estimates on individual-plant, entry-mean and plot bases, phenotypic and genetic correlations, expected response to selection, and correlated response to character selection.

Variance components for each trait were estimated from expected mean squares for the sources of variation C0/sets, C4/sets, env x C0/sets, env x C4/sets, C0 error, and C4 error, in the combined analyses of variance for Experiment II. Because of missing values for some entries in Experiment II,

$r_{C0} = 1.696$, $r_{C4} = 1.870$, $re_{C0} = 8.311$, $re_{C4} = 9.289$ for the traits grain yield, seeds/panicle, and panicles/plant instead of r = 2 and re = 10.

Standard errors of variance components were computed by using the formula:

$$\sqrt{\frac{2}{c^2}(M.S._i^2/df_i + 2)}$$

where c = coefficient of the component in the expected mean squares; $M.S._i$ = mean square for the i^{th} trait; df_i = degrees of freedom for the i^{th} trait.

Heritability values were calculated on an entry-mean basis and a plot basis, using the ratio of genetic variance (σ_g^2) to phenotypic variance (σ_{ph}^2). Heritabilities and their standard errors were estimated for the S_1 families for both the C0 and C4 cycles by using the following formulae:

Entry mean basis:

$$\frac{\hat{\sigma}_g^2}{\frac{\hat{\sigma}^2}{rn} + \frac{\hat{\sigma}_{ge}^2}{n} + \hat{\sigma}_g^2} \qquad S.E. = \frac{S.E.\hat{\sigma}_g^2}{\frac{\hat{\sigma}^2}{rn} + \frac{\hat{\sigma}_{ge}^2}{n} + \hat{\sigma}_g^2}$$

Plot basis:

$$\frac{\hat{\sigma}_g^2}{\hat{\sigma}^2 + \hat{\sigma}_{ge}^2 + \hat{\sigma}_g^2} \qquad S.E. = \frac{S.E.\hat{\sigma}_g^2}{\hat{\sigma}^2 + \hat{\sigma}_{ge}^2 + \hat{\sigma}_g^2}$$

Heritabilities were calculated on an individual-plant basis for the characters grain yield and 100-seed weight by

using the parent-offspring regression method. The regression coefficient $b = \frac{\sigma_{xy}}{\sigma_x^2}$, where x = the individual S_0 plant measurement minus the mean of all harvested plants from that cell of the isolation grid, and y = S_1 family mean over all environments minus the mean of all members of the same set.

After the correction for environmental effects, the x and y values were transformed to standard units by subtracting the means for all locations and dividing by the standard deviation to correct for differences in units of measure. Therefore, b provides a broad-sense heritability estimate equal to $\frac{\sigma_A^2 + \frac{1}{2}\sigma_D^2 + \sigma_{AA}^2 + \cdots}{\sigma_{ph}^2}$. Standard errors of the individual-plant heritabilities were calculated as S.E. b.

Genetic correlations among traits were calculated by using mean products and the estimates of genetic variance obtained from the combined analyses of variance. The formula was:

$$r_g = \frac{\sigma_{g_{xy}}}{\sqrt{\hat{\sigma}^2_{g_x}\ \hat{\sigma}^2_{g_y}}} \quad ,$$

where $\sigma_{g_{xy}}$ = the genetic covariance between traits x and y; $\hat{\sigma}^2_{g_x}$ and $\hat{\sigma}^2_{g_y}$ = estimates of genetic variance for traits x and y, respectively.

Estimated response to selection obtained by recombining selected families was calculated by using a basic formula, which may be modified to account for different selection procedures, and different numbers of generations per year and per cycle (Sprague and Eberhart, 1977). This formula is $G = k\ c\ \sigma_{ph}\ h^2$, where G = expected gain from selection; k = standardized selection differential; c = parental control value; σ_{ph} = square root of the phenotypic variance; and h^2 = heritability.

When using either gridded mass selection or S_1 family selection, k = 1.40 assuming a 20% selection intensity (Allard, 1960). For gridded mass selection of male-sterile plants (1 year/cycle) c = ½, due to control of only the female parent. For alternating gridded mass selection of male-sterile and fertile plants (2 years/cycle) c = ½ when male-sterile plants are selected (1st year) and c = 1 (due to control of both parents) when fertile plants are selected (2nd year). When S_1 family selection is practiced c = 1 because there is control of both parents. The b value obtained from the parent-offspring regression is considered an estimate of heritability for either of the types of mass selection. S_1 family genetic variance divided by S_1 family phenotypic variance is considered an estimate of heritability for S_1 selection.

Correlated responses to selection were calculated by

using the formula:

$$CR_{y(x)} = k_x \cdot \sqrt{h_x^2 \cdot r_{g_{x,y}} \cdot \sigma_{g_y}} \quad ,$$

where $CR_{y(x)}$ = expected correlated response in trait y when selection is applied to trait x; k_x = standardized selection differential (1.4 = 20% selection intensity) applied to trait x; $\sqrt{h_x^2}$ = square root of the heritability of trait x; $r_{g_{x,y}}$ = genetic correlation between traits x and y; and σ_{g_y} = square root of the estimate of genetic variance for trait y.

RESULTS

Environmental conditions generally were favorable for sorghum growth and development during 1982 and 1983. Frequent rains in late spring delayed planting in 1982, but they provided ample soil moisture and good seedbeds at all locations. Cool temperatures that prevailed in June were offset by high temperatures in July and midbloom occurred near the usual time. Cool temperatures returned in August and lasted until harvest, retarding grain filling and maturation. Grain yields for Experiments I and II at Ames in 1982 averaged 69.1 and 66.8 q/ha, respectively. At Beaconsfield, grain yields were much lower, 50.8 and 44.9 q/ha, respectively for Experiments I and II. The effects of cool temperatures and slow growth were especially evident at Sutherland in 1982 where mean grain yields were 32.6 q/ha for Experiment I and 32.5 q/ha for Experiment II.

In 1983, both experiments were seeded near the usual time for sorghum planting in Iowa, but dry seedbeds resulted in uneven emergence of the plants in some plots. Rainfall in mid-June provided for the emergence of additional seedlings and adequate stands were achieved in most plots. High temperatures prevailed from mid-June through September resulting in rapid plant growth and earlier than normal maturity. The Ames location received periodic rains, resulting in favorable growing conditions and good grain yields (85.2

q/ha for Experiment I and 70.7 q/ha for Experiment II). Beaconsfield, however, received only 0.73 inch of rain in July and August, resulting in low yields for both Experiments I and II (48.6 and 47.1 q/ha, respectively). The effects of an extended period of hot weather, coupled with poor stands in many plots at Sutherland in 1983, resulted in the decision not to harvest either experiment at that location for grain yield determinations.

In addition to the diverse and erratic environmental conditions in 1982 and 1983, growth conditions in 1977 indirectly affected both experiments. Seed for the C0 S_1 bulk in Experiment I and the 60 C0 S_1 families in Experiment II was obtained from the 1977 isolation planting of IAP3BR(M). Cool, wet conditions prevailed during August of that year, resulting in marked delays in anthesis and grain filling. Consequently, the seed harvested was abnormally small (Appendix Table A1), with some genotypes not reaching full maturity before the first autumn frost. As a result of these adversities, germination and seedling emergence of the C0 seed was poor in many plots.

Experiment I

Experiment I was designed to examine the changes that occurred in IAP3BR(M) during four cycles of selection for heavy 100-seed weight. The basic difference between the S_1

and half-sib family bulks used in Experiment I would be the amount of inbreeding. The S_1 family bulks were derived from fertile panicles which are primarily self-pollinated (ca. 94%) and have an inbreeding value, F, equal to 0.5. The half-sib (HS) family bulks were derived from male-sterile panicles which are cross pollinated and have an inbreeding value, F, equal to 0.

All plots in Experiment I were overseeded and thinned to achieve final stands of 4 plants/30 cm (1 ft) in 1982 and 3 plants/30 cm in 1983. Some entries, however, did not establish full stands, resulting in a number of short plots and six missing plots for the characters grain yield, seeds/panicle, and panicles/plant. Corrections were made for the short and missing plots. Individual-plot data were analyzed first on an individual-location basis, and then combined over the three locations (Ames, Beaconsfield, and Sutherland) and two years (1982 and 1983). Means for the individual-year-location data and their analyses of variance are provided in the Appendix for reference (Tables A2 through A8).

The combined analyses of variance (Table 6) indicate that the variation attributable to environments was highly significant ($P<0.01$) for grain yield and its primary components: 100-seed weight, seeds/panicle, and panicles/plant. The environment mean squares were strikingly larger than those for other sources of variation for grain yield, seeds/

Table 6. Mean squares from the combined analyses of variance for 100-seed weight, grain yield, seeds/panicle, panicles/plant, days to midbloom, and plant height for Experiment I, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Source of variation	df	100-seed weight ($x10^{-1}$)	df	Grain yield (x10)
Environments (env)	5	441.7**	4	117.0**
Replications/env	18	10.3	15	0.7
S_1 vs HS bulks	1	201.5	1	30.5*
HS linear	1	149.3**	1	3.7*
HS quadratic	1	9.7	1	3.1*
HS cubic	1	53.9*	1	0.6
S_1 linear	1	30.1	1	0.0
S_1 quadratic	1	8.7	1	0.3
S_1 cubic	1	22.2	1	0.0
S_1 vs HS x env	5	31.6**	4	2.5**
Cycles within S_1 and HS bulks x env	30	11.6	24	0.6
Error	126	9.5	98	0.5
C.V. (%)		10.7		12.6

[a]Measured only at Ames.

*,**Indicate significance beyond the 0.05 and 0.01 probability levels, respectively, in this and all subsequent tables.

Seeds/ panicle (x100)	Panicles/ plant ($x10^{-1}$)	df	Days to midbloom[a]	Plant height[a] (x10)
164.7**	498.0**	1	0.3	1.1
4.1	7.8	6	1.1	3.1**
17.4	28.4	1	6.3	65.2
12.9	12.3	1	33.3**	8.9
0.3	7.4	1	9.0	1.4
17.4	7.4	1	2.3	3.7
10.9	3.4	1	7.4	9.5
10.3	11.9	1	0.4	8.2
2.9	0.1	1	7.1	1.8
9.7	13.9**	1	0.6	1.5
4.6	3.4	6	2.4	1.8*
4.3	3.7	42	3.7	0.6
16.6	13.7		2.8	4.7

panicle, and panicles/plant, but not for 100-seed weight. Variation attributable to replications/environments was significant for only one trait, plant height.

Indications of the effects of inbreeding for each character are provided by the source of variation attributed to S_1 vs HS bulks (Table 6). If inbreeding is important, significant differences should be noted between the S_1 and HS bulks. Grain yield was the only character that showed significant ($P<0.05$) inbreeding depression.

The S_1 and HS bulk sources of variation were partitioned into component sources due to linear, quadratic, and cubic effects. These effects indicate whether changes occurred in trait means over cycles when selection was for 100-seed weight. The means for entries grouped by family cycle in Table 7 show whether the changes were in a desirable direction.

For the HS bulks, highly significant ($P<0.01$) linear effects were shown for 100-seed weight and days to midbloom, and significant ($P<0.05$) linear effects were noted for grain yield (Table 6). Grain yield also showed significant quadratic effects, and significant cubic effects were noted for 100-seed weight. The HS means in Table 7 reflect the linear cubic trends for 100-seed weight. Mean 100-seed weight increased in each cycle, except for a slight decrease in C3 (2.76, 3.06, 2.97, and 3.15 g). Similarly, grain yield

Table 7. Means for entries grouped by family-cycle for grain yield, 100-seed weight, seeds/panicle, panicles/plant, days to midbloom, and plant height for Experiment I, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Family-cycle	Grain yield (q/ha)	100-seed weight (g)	Seeds/ panicle	Panicles/ plant	Days to midbloom[a]	Plant height[a] (cm)
HS-C1	57.2	2.76	1352	1.4	65	168
HS-C2	60.0	3.06	1234	1.4	67	171
HS-C3	65.8	2.97	1333	1.5	69	185
HS-C4	60.8	3.15	1192	1.4	68	180
S1-C0	52.6	2.66	1305	1.4	67	143
S1-C2	53.7	2.87	1151	1.4	68	164
S1-C3	51.6	2.76	1198	1.4	67	158
S1-C4	49.1	2.84	1194	1.3	69	158
LSD (0.05), among HS or among S1 cycles	4.9	0.20	140	0.12	1.9	16

[a]Measured only at Ames.

increased the first three cycles (57.2, 60.0, and 65.8 q/ha) and then decreased in C4 (60.8 q/ha), demonstrating the linear and quadratic effects. The significant linear effect for days to midbloom was confirmed by the means in Table 7, because the HS bulks generally became later in succeeding cycles (65, 67, 69, and 68 days).

Significant linear, quadratic, or cubic effects were not indicated for the S_1 bulks (Table 6). A perusal of the S_1 cycle means shows that changes which occurred lacked a definite pattern for most traits, indicating that S_1 bulks may not serve as well as the HS bulks for sampling and subsequent evaluation of a population. Two factors could contribute to this conclusion. First, the unit for advancement of each cycle in IAP3BR(M) was a composite of male-sterile panicles (half-sibs), and effects of inbreeding may bias the results when S_1 bulks are used as the unit of evaluation. Secondly, the sample used to represent the population may not have been adequate. Each experimental unit consisted of a 3 m row containing 30 to 40 plants and these units were used to estimate parameters for the entire population. The source of variation attributable to replications/environments was non-significant for all characters except plant height. This suggests that inbreeding effects more likely had an impact on the differential performance of the S_1 and HS bulks.

Highly significant differences ($P<0.01$) for the S_1 vs

HS x environments mean squares for 100-seed weight, grain yield, and panicles/plant (Table 6) indicated there were changes in the ranking or magnitude of performance of the S_1 and HS bulks across environments. Significant ($P<0.05$) changes for the component cycles within S_1 and HS bulks across environments occurred only for plant height. Coefficients of variation ranged from 2.8% for days to midbloom to 16.6% for seeds/panicle. These percentages are similar to values obtained in other experiments with grain sorghum in Iowa in recent years.

Table 8 presents character means by family type, together with estimates of total inbreeding depression. Significant ($P<0.05$) differences between the HS and S_1 families occurred only for grain yield, where the HS bulks yielded 60.8 q/ha, S_1 bulks yielded 51.8 q/ha, and total inbreeding depression was estimated at -29.6%. Appreciable amounts of inbreeding depression also occurred for plant height (-22.7%), 100-seed weight (-14.0%), and seeds/panicle (-10.2%), but none of these reductions was significant beyond the 0.05 level of probability. In general, the HS bulks had heavier 100-seed weights, more seeds/panicle, and taller plants than S_1 bulks, but the differences were not significant beyond $P<0.05$.

Realized heritability for 100-seed weight was estimated by using the method described by Falconer (1981). Generation

Table 8. Character means by family type, least significant difference, and estimates of total inbreeding depression from S0 to S∞ for Experiment I, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Character	Mean HS	Mean S1	LSD (0.05)	Estimate of total inbreeding depression (%)	F test[a]
Yield (q/ha)	60.8	51.8	7.0	-29.6	*
100-seed weight (g)	2.99	2.78	0.21	-14.0	ns
Seeds/panicle	1278	1213	137	-10.2	ns
Panicles/plant	1.4	1.4	0.16	0.0	ns
Days to midbloom[b]	67	68	2.4	3.0	ns
Plant height (cm)[b]	176	156	39	-22.7	ns

[a]S1 vs HS. ns = nonsignificant.

[b]Measured only at Ames.

means for each cycle of selection for the HS bulks (Y) were plotted against the cumulative selection index (X) (Table 9). This procedure was used only for 100-seed weight because that was the trait undergoing direct selection. Data for HS bulks were used for the cycle means because selection and recombination units over cycles were HS families. The estimated heritability has no predictive value because it was calculated by using the observed results from cycle to cycle. The average value of the ratio R/S (where R = response to

Table 9. Values used to compute realized heritability for 100-seed weight as the slope of the regression of cycle means (Y) on cumulative selection index (X) for Experiment I, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

HS cycle	(X) Cumulative selection index (g)	(Y) 100-seed weight (g)
1	0.26	2.76
2	1.11	3.06
3	1.80	2.97
4	2.58	3.15

selection, and S = the selection differential) is given by the slope of the regression line fitted to the data points presented in Table 9. The regression equation fitted was $Y = 2.78 + 0.14X$, and realized heritability for 100-seed weight was estimated at 0.14 ± 0.08.

Experiment II

The plots in Experiment II were overseeded and subsequently thinned to 4 plants/30 cm in 1982 and 3 plants/30 cm in 1983. Variable environmental conditions coupled with poor germination and/or seedling emergence resulted in inadequate numbers of plants in some plots at all locations. My intent was to measure attributes on 60 C0 and 60 C4 S_1

families for all characters. This was accomplished for 100-seed weight, days to midbloom, plant height, and head type. Because of poor stands in some plots, however, only 49 C0 and 58 C4 S_1 families were analyzed in the combined ANOVA for grain yield, seeds/panicle, and panicles/plant. Individual-plot data were analyzed first on an individual-location basis, and then combined over the three locations (Ames, Beaconsfield, and Sutherland) and two years (1982 and 1982). Means for the individual-year location data and their analyses of variance are provided in the Appendix for reference (Tables A9 through A16).

Experiment II was designed to examine changes in character means, genetic variances, heritabilities, correlations among characters, expected gains from selection, and correlated responses to selection, between the initial (C0) and fourth (C4) cycle of IAP3BR(M). Differences in performance between the cycles may be attributed to the effects of gridded mass selection for large seed (i.e., heavy 100-seed weight).

The combined analyses of variance (Table 10) indicate that the variation attributable to environments was highly significant ($P<0.01$) for grain yield and its primary components (100-seed weight, seeds/panicle, and panicles/plant), and these mean squares were considerably larger than those for other sources of variation. Large differences in character means among the locations (Appendix Table A10) and

Table 10. Mean squares from the combined analyses of variance for 100-seed weight, grain yield, seeds/panicle, panicles/plant, days to midbloom, plant height, and panicle type for Experiment II, grown at Ames, Beaconsfield and Sutherland, in 1982 and 1983

Source of variation	Mean squares			
	df	100-seed weight ($x10^{-1}$)	df	Grain yield
Environments (env)	5	2535.4**	4	49038.2**
Replications (rep)/env	6	44.5**	5	474.9**
Sets/rep	10	109.5**	10	75.1
Genotypes/sets	114	109.2**	101	241.9**
C0 vs C4/sets	6	452.0**	6	768.6**
C0/sets	54	96.7**	43	165.1**
C4/sets	54	83.6**	52	244.6**
Sets/rep x env	50	12.4*	40	94.8**
Genotypes/sets x env	570	11.8**	393	62.0**
C0 vs C4/sets x env	30	18.3**	24	51.8
C0/sets x env	270	10.0	164	69.2**
C4/sets x env	270	12.8**	205	57.3**
Error	684	8.6	399	41.1
C0 vs C4 pooled error	36	8.0	30	51.5
C0 pooled error	324	8.7	145	46.3
C4 pooled error	324	8.6	224	36.4
All entries C.V. (%)		12.6		15.2
C0 entries C.V. (%)		12.1		15.4
C4 entries C.V. (%)		12.5		15.1

[a]Measured only at Ames.

[b]Measured only in 1983.

Mean squares						
Seeds/ panicle (x100)	Panicles/ plant	df	Days to midbloom[a]	Plant height[a] (x10)	df	Panicle type[b]
873.5**	20.72**	1	125.1	6.4	2	9.0
6.5	0.05*	2	16.8**	21.2**	3	1.5**
20.5*	0.14**	10	13.3	10.9	10	1.5**
40.7**	0.14**	114	26.5**	13.6**	114	3.2**
189.9**	0.11*	6	70.3**	20.5*	6	2.4**
35.7**	0.11**	54	11.3**	12.2**	54	2.3**
27.7**	0.17**	54	36.8**	14.1**	54	4.2**
8.4**	0.04**	10	6.7**	4.3**	20	0.4**
5.7	0.04**	114	2.7*	2.2**	228	0.3**
4.8	0.03	6	2.0	4.2*	12	0.3
7.4	0.04**	54	22.0	2.1*	108	0.4**
4.4	0.04**	54	3.5	2.1**	108	0.3**
5.1	0.02	228	2.0	1.3	342	0.2
9.0	0.03	12	2.0	1.3	18	0.2
6.3	0.02	108	1.4	1.4	162	0.2
3.7	0.02	108	2.6	1.1	162	0.2
18.2	15.0		2.4	9.4		21.1
19.1	14.7		2.1	9.4		23.6
17.1	15.2		2.7	9.0		18.7

differences in plant populations in the two years contributed to the large mean squares for environments. The replications/environment source of variation was significant ($P<0.05$) or highly significant ($P<0.01$) for all traits except seeds/panicles. Variation due to sets/replications was highly significant for 100-seed weight, panicles/plant, and head type, and significant for seeds/panicle.

Differences among genotypes/sets were highly significant ($P<0.01$) for all traits. There were significant differences between C0 and C4 S_1 families/sets for panicles/plant and plant height, and highly significant differences for all other traits. Differences among S_1 families in the C0 and C4 were highly significant for all traits.

Genotype/sets x environment interactions were highly significant for 100-seed weight, grain yield, panicles/plant, plant height, and head type, significant for days to mid-bloom, and not significant for seeds/panicle. A partitioning of the genotype x environment source of variation into component parts indicated that the C0 vs C4/sets x environment and C4/sets x environment sources of variation were responsible for the significant differences in 100-seed weight. Variations for C0/sets x environment and C4/sets x environment were significant ($P<0.01$) for grain yield, panicles/plant, and head type, but the C0 vs C4 sets x environments mean squares were not significant for those traits. All component

sources of variation contributed to the significance of differences in plant height.

Coefficients of variation for the analyses that involved all entries ranged from 2.4% for days to midbloom to 21.1% for head type. Ranges in coefficients of variation for the data within individual cycles (C0 and C4) were similar. The percentages are higher for most traits than those recorded in Experiment I. The low CVs for days to midbloom and plant height may reflect the fact that these traits were recorded only at Ames. Primary interest in this research lies with 100-seed weight; therefore, it is gratifying that among grain yield and its components, 100-seed weight had the lowest CVs.

If recurrent selection is effective and theory relative to its use is correct, the population mean should shift favorably for the trait under selection, while variability for that trait is maintained. Further, the mean and variance for traits not under selection should not change if those traits are not correlated with the trait under selection and population size is not considered finite. Means, ranges, and variance estimates also allow the plant breeder to assess the potential value of a population as a source for the development of inbred lines or synthetic varieties.

Population means and ranges for all entries, and for the C0 and C4 cycles individually, are presented in Table 11.

Table 11. Means, high and low genotype values, and genotype L.S.D.(.05) for characters measured in the combined ANOVA for Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Character	Genotype values		
	Mean		
	All entries	C0	C4
Grain yield (q/ha)	52.0 ± 2.6	54.2 ± 2.9	50.3 ± 2.5
100-seed weight (g)	2.74 ± 0.10	2.61 ± 0.09	2.86 ± 0.10
Seeds/panicle	1310 ± 80	1423 ± 94	1224 ± 69
Panicles/plant	1.3 ± 0.07	1.4 ± 0.07	1.3 ± 0.07
Days to midbloom[b]	68.2 ± 0.8	67.2 ± 0.7	69.2 ± 0.9
Plant height[b] (cm)	157.2 ± 7.4	154.3 ± 7.3	160.7 ± 7.2
Panicle type[c]	2.7 ± 0.23	2.6 ± 0.3	2.8 ± 0.2

[a]Difference in genotype means needed for significance at 0.05 probability level.

[b]Measured only at Ames.

[c]Measured only in 1983.

Genotype values								
High			Low			Genotype L.S.D. (.05)[a]		
All entries	C0	C4	All entries	C0	C4	All entries	C0	C4
106.2	106.2	99.9	14.1	15.0	14.1	7.4	8.1	7.0
4.44	4.22	4.44	1.21	1.21	1.44	0.28	0.26	0.29
2872	2872	2405	581	732	581	225	263	193
2.8	2.8	2.8	0.5	0.7	0.5	0.19	0.19	0.18
79.0	74.0	79.0	62.0	62.0	62.0	2.3	2.0	2.6
220.0	220.0	220.0	95.0	98.0	95.0	21.0	20.5	20.4
4.0	4.0	4.0	1.0	1.0	1.0	0.7	0.7	0.6

Four cycles of selection for seed size in IAP3BR(M) were effective in shifting the mean for 100-seed weight from 2.61 to 2.86 g. Mean 100-seed weights of the S_1 family bulks in the C0 and C4 in Experiment I were 2.66 and 2.84, respectively (Table 7). Concurrently, decreases were noted between the C0 and C4 (Table 11) in grain yield (54.2 to 50.3 q/ha), seeds/panicle (1423 to 1224), and panicles/plant (1.4 to 1.3). In contrast, increases occurred between the C0 and C4 for days to midbloom (67.7 to 69.2), plant height (154.3 to 160.7 cm), and openness of panicle (2.6 to 2.8).

Ranges between the high and low genotype values (Table 11) narrowed between the C0 and C4, from 91.2 to 85.8 q/ha for grain yield and from 2140 to 1824 for seeds/panicle. Increased ranges were noted from C0 to C4 between the high and low genotype values for days to midbloom (from 12 to 17 days), plant height (from 122 to 125 cm), and panicles/plant (from 2.1 to 2.3 panicles). The range between high and low genotype values remained constant from the C0 to C4 for 100-seed weight (3.01 g vs 3.00 g). Despite changes in range between the high and low genotype values, the population maintained a large amount of variability for all characters after four cycles of selection for 100-seed weight.

Estimates of variance components are presented in Table 12. Error variances (σ^2) for most traits were relatively large and greater than the estimates of genotype-environment

Table 12. Estimates of variance components for characters measured in Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Character	Cycle	Variance component			
		σ^2	σ^2_{ge}	σ^2_g	σ^2_{ph}
Grain yield (q/ha)	C0	46.30 ± 5.40	13.52 ± 5.50	11.53 ± 4.29*	19.86 ± 4.19
	C4	36.36 ± 3.42	11.21 ± 3.53	20.16 ± 5.10*	26.33 ± 5.07
100-seed weight ($\times 10^{-1}$) (g)	C0	8.70 ± 0.68	0.65 ± 0.55**	7.23 ± 1.52	8.06 ± 1.52
	C4	8.60 ± 0.67	2.10 ± 0.64**	5.90 ± 1.32	6.97 ± 1.32
Seeds/panicle (x 100)	C0	6.3 ± 0.7*	0.6 ± 0.6**	3.4 ± 0.9	4.3 ± 0.9
	C4	3.7 ± 0.4*	0.3 ± 0.3**	2.5 ± 0.6	3.0 ± 0.6
Panicles/plant ($\times 10^{-1}$)	C0	2.0 ± 0.2	1.2 ± 0.3	0.8 ± 0.3**	1.3 ± 0.3
	C4	2.0 ± 0.2	1.1 ± 0.2	0.1 ± 0.0**	1.8 ± 0.4
Days to midbloom[a]	C0	1.4 ± 0.2*	0.3 ± 0.2*	2.32 ± 0.5**	2.8 ± 0.5**
	C4	2.6 ± 0.3*	0.5 ± 0.4*	8.32 ± 1.7**	9.2 ± 1.7**
Plant height[a] (x 10) (cm)	C0	1.4 ± 0.2	0.4 ± 0.2	2.5 ± 0.6	3.1 ± 0.6
	C4	1.1 ± 0.2	0.5 ± 0.2	3.0 ± 0.7	3.5 ± 0.7
Panicle type[b]	C0	0.2 ± 0.03	0.07 ± 0.03	0.3 ± 0.07**	0.4 ± 0.07
	C4	0.2 ± 0.02	0.07 ± 0.02	0.7 ± 0.13**	0.7 ± 0.13*

[a]Measured only at Ames.

[b]Measured only in 1983.

variance (σ^2_{ge}), genotypic variance (σ^2_g), and phenotypic variance (σ^2_{ph}) for grain yield and the primary components of yield. Significant differences ($P<0.05$) in error variance between the C0 and C4 were noted for seeds/panicle and days to midbloom. For all traits except days to midbloom, the C0 error variance was greater than or equal to the C4 error variance. Differences between cycles for the genotype-environment variance were highly significant for 100-seed weight and seeds/panicle, and they were significant for days to midbloom. The differences for 100-seed weight and days to midbloom were due to an increase in the g x e variance between the C0 and C4, while the difference for seeds/panicle was the result of a decrease. These results indicate that the lines may be more stable across environments for seeds/panicle as selection progressed, but they may be less stable for 100-seed weight and days to midbloom. This does not preclude the possibility of selecting lines that are stable across environments from either the C0 or the C4.

Genotypic variance is very important to the plant breeder when a population is undergoing recurrent selection. Decreases in genotypic variance after several cycles of selection would indicate a narrowing of the genetic base for a given trait. In IAP3BR(M), grain yield showed a significant ($P<0.05$) increase in genotypic variance from the C0 to the C4, while days to midbloom and panicle type showed highly signifi-

cant ($P<0.01$) increases. Conversely, panicles/plant showed a highly significant decrease in genotypic variance between these cycles. Differences in genotypic variance between the C0 and C4 were not significant for 100-seed weight and seeds/panicle. However, for both characters the estimates of σ_g^2 were smaller for the C4 than the C0. Highly significant ($P<0.01$) and significant ($P<0.05$) differences in phenotypic variance were noted for days to midbloom and panicle type, respectively.

The variance-component estimates presented in Table 12 were used to calculate heritability values on a plot and on a progeny-mean basis. Individual-plant heritabilities also were calculated by using the parent-offspring regression method. The regression estimates were made only for grain yield and 100-seed weight, using data obtained from the 1977 and 1981 isolation plantings. The three types of heritability estimates are presented in Table 13.

Heritabilities on a progeny-mean basis were high for most characters, ranging from 0.19 for panicles/plant in the C4 to 0.93 for panicle type in the C4. It is noteworthy that the heritability for 100-seed weight decreased slightly from the C0 to C4, while most other traits (i.e., those not under selection) showed increased heritability from the C0 to C4. Heritabilities on a plot basis showed similar trends from C0 to C4, but the estimates were smaller, ranging from 0.03

Table 13. Estimates of heritabilities for characters measured in Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Character	Heritability	
	C0	C4
Plot basis		
Grain yield/unit area	0.16 ± 0.06	0.30 ± 0.08
100-seed weight	0.44 ± 0.09	0.36 ± 0.08
Seeds/panicle	0.33 ± 0.09	0.39 ± 0.09
Panicles/plant	0.20 ± 0.08	0.03 ± 0.00
Days to midbloom[a]	0.58 ± 0.13	0.73 ± 0.15
Plant height[a]	0.58 ± 0.14	0.65 ± 0.15
Panicle type[b]	0.50 ± 0.17	0.70 ± 0.13
Progeny-mean basis		
Grain yield/unit area	0.58 ± 0.22	0.77 ± 0.19
100-seed weight	0.90 ± 0.19	0.85 ± 0.19
Seeds/panicle	0.79 ± 0.21	0.84 ± 0.19
Panicles/plant	0.64 ± 0.22	0.19 ± 0.19
Days to midbloom[a]	0.82 ± 0.19	0.91 ± 0.19
Plant height[a]	0.83 ± 0.19	0.85 ± 0.19
Panicle type[b]	0.83 ± 0.19	0.93 ± 0.19
Individual-plant basis[c]		
Grain yield/unit area	-0.12 ± 0.02	0.03 ± 0.00
100-seed weight	0.35 ± 0.05	0.39 ± 0.05

[a]Measured only at Ames.

[b]Measured only in 1983.

[c]Determined only from Ames data, 1977 and 1981.

for panicles/plant to 0.73 for days to midbloom. Extremely low h^2 values were obtained with both methods for panicles/plant in the C4. This may be due in part to the low estimate of σ_g^2 that was listed for that trait in Table 12.

Heritability of grain yield on an individual-plant basis was -0.12 in the C0 and 0.03 in C4, indicating that it would be difficult to improve grain yield by using data from individual plants. However, individual-plant estimates of heritability for 100-seed weight were of moderate magnitude (0.35 for C0 and 0.39 for C4), indicating that gridded mass selection may be useful for improving seed size in sorghum. For all methods of estimation and in both cycles of the population, grain yield usually was the least heritable trait. Panicles/plant and seeds/panicle most often had the next lowest estimates. 100-seed weight, days to midbloom, plant height, and panicle type all exhibited moderate to high heritability.

Estimates of variance components (Table 12), progeny-mean heritability values (Table 13), cycle means (Table 11), and a 20% selection intensity were used to calculate estimates of gain from S_1 family selection (Table 14). In the C0, estimated gain/year ranged from 1.0% of the mean for days to midbloom to 8.8% of the mean for head type. The estimated gain for 100-seed weight was 0.36 g/cycle or 4.6%/year. Grain yield estimates were low at 2.9 q/ha gain per cycle or 1.8%/year.

Table 14. Estimated gains from S_1 family selection for the C0 and C4, with a 20% selection intensity, for characters measured in Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Character selected	S_1 family selection (3 years/cycle) Estimated gain/cycle	Estimated gain/year	Estimated gain/year (% of mean)
	C0		
Yield (q/ha)	2.9	1.0	1.8
100-seed weight (g)	0.36	0.12	4.6
Seeds/panicle	230	77	5.4
Panicles/plant	0.10	0.03	2.4
Days to midbloom[a]	1.9	0.6	1.0
Plant height (cm)[a]	20.0	6.8	4.4
Panicle type[b]	0.7	0.2	8.8
	C4		
Yield (q/ha)	5.5	1.8	3.6
100-seed weight (g)	0.31	0.11	3.7
Seeds/panicle	203	68	5.6
Panicles/plant	0.02	0.01	0.5
Days to midbloom[a]	3.8	1.3	1.8
Plant height (cm)[a]	22.9	7.6	4.7
Panicle type[b]	1.1	0.4	12.9

[a]Measured only at Ames.

[b]Measured only in 1983.

Estimated gains determined from the C4 data ranged from 0.5% of the mean/year for panicles/plant to 12.9% of the mean/year for panicle type. The estimated gain for 100-seed weight dropped slightly from the C0 to 0.31 g/cycle or 3.7%/year in the C4. Surprisingly, the estimate for gain in grain yield almost doubled from the C0 to C4 (2.9 vs 5.5 q/ha/cycle). The C4 estimate represents a gain of 3.6%/year. The estimated gain for panicles/plant dropped considerably from 0.10 panicles/cycle in C0 to 0.02 panicles/cycle in the C4, probably a reflection of the marked reduction in σ_g^2 shown in Table 12. Slight increases in the expected gain as a percentage of the mean were noted between C0 and C4 for seeds/panicle, days to midbloom, plant height, and head type.

By using the heritability estimates on an individual-plant basis (Table 13), a 20% selection intensity, and data from individual fertile plants harvested in the 1977 and 1981 isolation plantings (Appendix Table A1), estimated gains from individual-plant selection were determined. The estimates for grain yield and 100-seed weight are shown in Table 15. All gains in grain yield determined from the C0 data were negative because of the negative heritability listed in Table 13. By using gridded mass selection of male-sterile plants, gains in 100-seed weight were estimated at 0.11 g/cycle or 4.2% of the mean/year in the C0 (Table 15). In the C4, estimated gains improved to 0.15 g/cycle, but the advance

Table 15. Estimated gains from individual-plant selection in the C0 and C4, for grain yield and 100-seed weight, using a 20% selection intensity based on S_0 plants[a] which gave rise to the families[b] of Experiment II

	Character selected and cycle			
	C0		C4	
Procedure	Grain yield/ main culm panicle (g)	100-seed weight (g)	Grain yield/ main culm panicle (g)	100-seed weight (g)
Gridded mass selection of male-sterile plants (1 yr/cycle)				
Gain/cycle	-0.64	0.11	0.34	0.15
Gain/year	-0.64	0.11	0.34	0.15
Estimated gain/year (% of mean)	-0.8	4.2	0.4	4.3
Alternating gridded mass selection of male-sterile and fertile plants (2 years/cycle)				
Gain/cycle	-1.93	0.34	1.01	0.44
Gain/year	-0.97	0.17	0.51	0.22
Estimated gain/year (% of mean)	-1.3	6.5	0.6	6.3

[a]Data for the S_0 plant estimates were from C0 plants grown in 1977 and C4 plants grown in 1981 at Ames.

[b]Data for the C0 and C4 families were from plots grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983.

still was only 4.3% of the mean/year. In the C4, grain yield showed a 0.34 g/panicle gain per year, which represents only 0.4% of the mean. By alternating gridded mass selection of male-sterile and fertile plants, gains/cycle and gains/year increased in all instances, as did the percentage gains/years.

Comparisons of the effectiveness of S_1 family selection and gridded mass selection for grain yield and 100-seed weight are provided by the data in Tables 14 and 15. S_1 family testing was decidedly the faster way to improve grain yield, according to either the C0 or C4 data. Although S_1 testing is more costly, it seems clearly the better choice because mass selection gave negative progress for grain yield in the C0 (-0.8% of the mean/year) and extremely little progress in the C4 (0.4% of the mean/year). Gridded mass selection for 100-seed weight in the C0 produced a gain almost equal to the gain estimated for S_1 family testing (0.11 vs 0.12 g/year). But in the C4, estimated gains from mass selection of male-sterile plants were superior to those for S_1 family testing (0.15 vs 0.11 g/year). When alternating selection of male-sterile and fertile plants was used, the gains per year in favor of mass selection were still greater. The better gains along with lower costs for mass selection make it a logical choice for improving 100-seed weight in sorghum.

Phenotypic and genetic correlations are presented in Tables 16 and 17 for the C0 and C4 data, respectively.

Table 16. Phenotypic (above diagonal) and genetic (below diagonal) correlations among characters measured in C0 from Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

	Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	Days to mid-bloom[a]	Plant height[a]	Panicle type[b]
Grain yield		0.33*	0.17	0.27	0.11	0.44**	0.04
100-seed weight	0.49		-0.72**	0.18	-0.04	0.51**	0.13
Seeds/panicle	0.15	-0.79		-0.48**	0.22	-0.23	0.03
Panicles/plant	0.22	0.24	-0.54		-0.39**	0.14	-0.01
Days to midbloom[a]	0.09	-0.02	0.30	-1.05		-0.09	-0.29*
Plant height[a]	0.94	0.69	-0.42	0.32	-0.15		0.20
Panicle type[b]	-0.04	0.18	0.12	-0.03	-0.46	0.30	

[a]Measured only at Ames.

[b]Measured only in 1983.

Table 17. Phenotypic (above diagonal) and genetic (below diagonal) correlations among characters measured in C4 from Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

	Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	Days to mid-bloom[a]	Plant height[a]	Panicle type[b]
Grain yield		0.06	0.40**	0.46**	0.06	0.47**	0.34*
100-seed weight	0.00		-0.78**	0.47**	0.01	0.25	-0.19
Seeds/panicle	0.44	-0.79		-0.47**	0.32*	-0.05	0.19
Panicles/plant	0.61	0.59	-0.50		-0.51**	0.28*	0.18
Days to midbloom[a]	0.10	0.03	0.38	-0.95		-0.19	-0.24
Plant height[a]	0.73	0.35	-0.08	0.45	-0.23		0.05
Panicle type[b]	0.62	-0.22	0.20	0.46	-0.19	0.06	

[a]Measured only at Ames.

[b]Measured only in 1983.

Correlations involving grain yield, seeds/panicle, and panicles/plant had 43 and 52 degrees of freedom in Tables 16 and 17, respectively. All other correlations in either Table 16 or 17 had 54 degrees of freedom. Although it is expected that means will change and variances will remain relatively constant when recurrent selection is practiced, changes may occur in the relationships among different characters after a population has progressed through several cycles of selection. Among the phenotypic correlations in the C0 (Table 16), grain yield was correlated positively with 100-seed weight ($r = 0.33$) and plant height ($r = 0.44$). 100-seed weight was correlated negatively with seeds/panicle ($r = -0.72$) and positively with plant height ($r = 0.51$). Seeds/panicle was correlated negatively with panicles/plant ($r = -0.48$), and panicles/plant in turn was correlated negatively with days to midbloom ($r = -0.39$). The negative correlation of days to midbloom with panicle type ($r = -0.29$) just reached the 0.05 probability level.

There were several differences among the C4 (Table 17) phenotypic correlations compared with those for the C0 (Table 16). Grain yield was no longer correlated significantly with 100-seed weight, but it was positively and significantly correlated with seeds/panicle ($r = 0.40$), panicles/plant ($r = 0.46$), and panicle type ($r = 0.34$). The phenotypic correlation of grain yield with plant height was nearly the

same in the two cycles (r = 0.44 in C0 and r = 0.47 in C4). Correlations between 100-seed weight and seeds/panicle were strong and negative in both cycles (r = -0.78 and -0.72). The correlation of 100-seed weight with plant height decreased in magnitude and was not significant in the C4. A highly significant positive correlation was shown for 100-seed weight with panicles/plant (r = 0.47). Seeds/panicle showed nearly the same negative correlation with panicles/plant in the C4 (r = -0.47) as it did in the C0 (r = -0.48). The negative correlation of panicles/plant with days to midbloom was stronger in the C4 (r = -0.51) than in the C0 (r = -0.39).

Genotypic correlations among most characters were similar in direction and magnitude to the phenotypic correlations, although the genotypic correlations tended to be somewhat higher for several traits. One comparison to that end is the correlation between days to midbloom and panicles/plant. Phenotypic correlations were r = -0.39 in C0 and r = -0.51 in C4, but the genotypic correlations were r = -1.05 in C0 and r = -0.94 in C4.

Correlated response to selection is a function of the response of a given character to selection and strength of the genetic correlation of that trait with other traits. Estimates of correlated response are presented for the C0 and C4 in Table 18, when S_1 family selection is practiced for

Table 18. Estimates of correlated response in other characters when S_1 family selection is for 100-seed weight, grain yield, seeds/panicle, and panicles/plant; responses are expressed as percentages of the expected gain from S_1 family selection for a given character, calculated from Experiment II, grown at Ames, Beaconsfield, and Sutherland, in 1982 and 1983

Selected character	Unselected character						
	100-seed weight	Grain yield	Seeds/panicle	Panicles/plant	Days to mid-bloom[a]	Plant height[a]	Panicle type[b]
			C0				
100-seed weight	100.0	26.0	-84.1	28.7	-3.2	70.9	18.7
Grain yield	39.5	100.0	12.8	21.2	7.6	77.5	-3.3
Seeds/panicle	-74.2	21.8	100.0	-60.7	29.4	-40.4	11.7
Panicles/plant	20.3	28.8	-48.5	100.0	-92.6	27.7	-2.6
			C4				
100-seed weight	100.0	0.0	-79.4	126.7	2.9	34.2	-33.9
Grain yield	0.0	100.0	42.1	124.7	9.2	67.7	59.0
Seeds/panicle	-78.4	46.1	100.0	-106.8	36.7	-7.8	19.9
Panicles/plant	55.7	60.8	-47.5	100.0	-87.2	41.6	43.4

[a]Measured only at Ames.

[b]Measured only in 1983.

100-seed weight, grain yield, seeds/panicle, and panicles/plant. The responses are expressed for each trait as percentage of the expected gain for S_1 family selection if selection were practiced directly for that trait. For example, when selection is for 100-seed weight in C0, simultaneous increases would be expected in grain yield (26.0%), panicles/plant (28.7%), plant height (70.9%), and the score for panicle type (18.7%). A marked decrease would be expected in seeds/panicle (-84.1%), and the number of days to midbloom should decrease slightly (-3.2%). From the C4 data, it was estimated that selection for 100-seed weight would produce little or no gain in grain yield (0.0%) and days to midbloom (2.9%), decreases in seeds/panicle (-79.4%) and the score for panicle type (-33.9%) and an increase in plant height (34.2%). The value of 126.7% for panicles/plant indicates that the increase should be greater than would be expected if selection were directly for panicles/plant.

Selection for grain yield should produce increases in 100-seed weight in C0 (39.5%), but no gain in C4 (0.0%). The estimates also indicate that gains would be expected for seeds/panicle, panicles/plant, plant height, and days to midbloom in either the C0 or C4 when selection was for grain yield. Usually, the gains estimated from the C0 data were less than those for the C4. Selection for seeds/panicle should result in similar correlated responses in the C0 and C4. One

could expect decreases in 100-seed weight, panicles/plant, and plant height, and increases in grain yield, days to midbloom, and openness of the panicles when selecting for more seeds/ panicle. Similar responses are shown in the C0 and C4 when selection is for panicles/plant. Concurrent increases would be expected for 100-seed weight, grain yield, and plant height and decreases should occur for seeds/panicle and days to midbloom.

Estimates from the C0 data indicate that direct selection for each character would produce the greatest gain for that character. In the C4, however, the estimates suggest that indirect selection for either grain yield, seeds/panicle, or 100-seed weight would give greater gains for panicles/plant than would direct selection for panicles/plant. For all other traits, direct selection in the C4 should produce the greatest gain for that trait. Among the primary components of yield, indirect selection for panicles/plant should give the greatest concurrent increase in grain yield.

DISCUSSION

IAP3BR(M)C4 is a large-seeded grain-sorghum population that has undergone four cycles of gridded mass selection for heavy 100-seed weight (large seed). The results from Experiments I and II, conducted over two years at three locations, provide a rather complete description of the performance and genetic variability of the population.

The effects of mass selection for heavy 100-seed weight were not consistent in Experiment I. Both linear and cubic responses over cycles were noted for the HS bulk populations (Table 6). The means for HS bulks in Table 7 show an increase in 100-seed weight between cycles in two of three instances, and the change from 2.76 g in C1 to 3.15 g in C4 was significant ($P \leq 0.05$). For the S_1 bulks, the responses over cycles usually were smaller. The change in S_1 means from 2.66 g in the C0 to 2.84 g in the C4 did not exceed the 0.05 probability level.

In Experiment II, the 60 S_1 families from the initial population and the fourth selection cycle provided data appropriate for the estimation of genotype and error variances. Significant differences were noted for all characters for the variation attributable to C0 vs C4 genotypes/sets (Table 10). The means in Table 11 show an increase in 100-seed weight from 2.61 g in the C0 to 2.86 g in the C4. The results are not striking in either experiment but they indicate that progress

was made in increasing 100-seed weight in the population by using gridded mass selection.

Two factors, inbreeding depression and sample size, could affect the usefulness of S_1 bulks in evaluating changes in this population. Inbreeding effects would tend to reduce heterozygosity in successive cycles and thereby influence the range between S_1 bulk means. The difference between the high and low means for the HS bulk cycles for 100-seed weight was 0.39 g, for example, while the difference between the high and low S_1 bulk means was 0.21 g (Table 7). Thus, the range among cycle values for the S_1 bulks was barely half that exhibited by the HS bulks. Because the HS bulk means had a greater range, and the same error term was used for testing the S_1 and HS bulks (Table 3), it seems that a greater number of significant differences would occur among the HS bulks.

To temper the effects of inbreeding, it would be desirable to sample a large number of individual S_1 families within each of the four cycles and test them extensively. Experiment II provided a markedly larger sample of the C0 and C4 populations than did Experiment I. Increased degrees of freedom associated with the larger sample in turn had a bearing on the power of the F-test, and may also have contributed to the significance indicated between the two cycles. Lack of significance among the S_1 bulks of Experiment I may have resulted partially from the effects of inbreeding and partially

from the relatively small sampling of the population. Although the estimates of S_1 mean 100-seed weight for the C0 and C4 in Experiments I and II were similar (Tables 7 and 11, respectively), the use of S_1 bulks may not serve well for the estimation of population trends over successive cycles.

Ross et al. (1971) emphasized that, for recurrent selection to be successful for a given character in sorghum, not only should there be a desirable change in the mean, but the genotypic variance should remain essentially constant. Ranges between the high and low values for 100-seed weight in Experiment II (Table 11) were nearly the same in the C0 (3.01 g/100 seeds) and C4 (3.00 g/100 seeds). The high-genotype value, however, shifted favorably (0.22 g/100 seeds increase) from C0 to C4 as did the total range of values. Although the ranges may serve as indicators of relative variability, more precise estimates are provided in Table 12. Genotypic variance (σ_g^2) for 100-seed weight decreased slightly from the C0 (7.23) to C4 (5.90), but the change was not significant statistically. The basic premises underlying progress with recurrent selection, therefore, have been upheld in this population: (1) the mean and range for the trait under selection have responded in a positive direction and (2) the genotypic variance has remained essentially constant.

Stability of performance in different environments is of concern to plant breeders when developing material destined

for a large area of adaption. Kambal and Webster (1965) found that GCA and SCA effects for 100-seed weight in sorghum were stable over environments and indicated that extensive testing over locations to evaluate that trait was not necessary. Similarly, Lothrop (1983) recommended gridded mass selection as a method to improve 100-seed weight because of the small genotype x environment interaction displayed by lines from the sorghum population IAP1R(M)C3. In tests that involved S_1 families, he found that σ^2_{ge} was 8% of σ^2_{ph} in one experiment and 22% of σ^2_{ph} in another.

In my experiments with IAP3BR(M), a highly significant difference in σ^2_{ge} for 100-seed weight was noted between the C0 and the C4 (Table 12). In the C0, σ^2_{ge} was 8% of σ^2_{ph}, but after four cycles of selection, σ^2_{ge} was 30% of σ^2_{ph}. Considering the σ^2_{ge} values specifically, lines from the C0 were more stable across environments than those from the C4. S_1 families in the initial cycle (C0) would not be expected to exhibit a large σ^2_{ge} because the 30 lines used in constituting IAP3BR(M) were developed in several sorghum breeding projects dispersed throughout the central United States. The initial compositing of crosses to these lines should produce a population that would be quite heterogeneous and stable over different environments. It may be that selection for large seed over four cycles at Ames resulted in concurrent selection for genotypes best adapted to the Ames environment. In

turn, this may be reflected in the significantly greater estimate of σ^2_{ge} in the C4 for evaluations made over six environments.

The significant decrease in σ^2_{ge} for seeds/panicle seems noteworthy (Table 12). The value in the C4 is half that of the C0, indicating appreciably greater stability for this trait in the C4. The strong negative correlations between 100-seed weight and seeds/panicle shown for both cycles of the population (Tables 16 and 17) point up a yield component relationship that likely had a depressing effect on the σ^2_{ge} value for seeds/panicle as selection for 100-seed weight progressed.

Caution should be exercised in drawing conclusions about relative stability of lines tested in the two cycles. The increase in σ^2_{ge} for 100-seed weight and the decrease shown for seeds/panicle between the C0 and C4 could result from the disproportionate impact of only a few highly diverse S_1 families. Additionally, although the σ^2_{ge} estimates have increased for some traits and decreased for others from the C0 to C4, it should be possible to select individual lines from either cycle that would be stable across environments. The increase in σ^2_{ge} for 100-seed weight over the selection cycles suggests that evaluations for the stability of that trait should be made in several environments, even though gridded mass selection at one location has been effective in

the improvement of mean seed size.

Population means for quantitatively inherited traits may show appreciable change with inbreeding. Large amounts of inbreeding depression indicate that a large proportion of nonadditive gene action is being expressed for the trait under consideration, because the heterozygote has a greater value than the homozygote. Small amounts of inbreeding depression indicate that inheritance of the trait is controlled primarily by additive gene action. Estimates of inbreeding depression in sorghums would be expected to be low because it is predominantly self-pollinated.

Direct estimates of dominance variance were not obtained in my experiments because dominance variance is compounded with additive variance in S_1 families ($\sigma^2_{S_1} = \sigma^2_{A*} + \frac{1}{4}\sigma^2_D$), and HS families only provide an estimate of the additive variance ($\sigma^2_{HS} = \frac{1}{4}\sigma^2_A$). Nonadditive gene action was estimated indirectly in Experiment I, however, by determining the inbreeding depression from S_0 to S_∞ (100% homozygosity).

Inbreeding depression for 100-seed weight in IAP3BR was estimated at 14% (Table 8). That value is approximately three times the 4.9% that was estimated by Lothrop (1983) for IAP1R sorghum population. Malm (1968) and Laosuwan and Atkins (1977) evaluated the performance of hybrid sorghums that involved either unadapted or exotic parental materials and found that additive gene effects were of major importance

in the inheritance of seed size. However, investigations that involved parents that were more adapted to the area indicated that nonadditive gene action also contributed appreciably to the expression of seed size (Niehaus and Pickett, 1966; Beil and Atkins, 1967; Liang and Walter, 1968). The greater inbreeding depression for IAP3BR in comparison with IAP1R may reflect greater adaptability of the parental materials as well as the markedly heavier 100-seed weight of most parents. Even with inbreeding depression of 14%, my results indicate that 100-seed weight is controlled primarily by additive gene effects, and they support the findings of Lothrop (1983) and Jan-Orn et al. (1976).

Sorghum breeders may also wish to know (1) the potential of IAP3BR(M)(C4) for continued improvement in 100-seed weight and (2) what the most efficient method of selection might be. Comparisons of the heritability estimates and genetic variances determined from the C0 and C4 data may provide answers to these questions. Heritabilities in the C4 for 100-seed weight were lower than those for the C0 on a progeny-mean and plot basis, but higher on an individual-plant basis (Table 13). Progeny-mean heritabilities in the C0 (0.90) and C4 (0.85) were in close agreement with those reported by Lothrop (1983) for third cycle S_1 families of IAP1R (0.82 and 0.78 in two experiments) and Eckebil et al. (1977) (0.86, 0.87, and 0.91 for S_1 lines from three populations). The individual-plant

heritabilities for 100-seed weight in my experiments (0.35 in C0 and 0.39 in C4) were slightly lower than those reported by Lothrop (1983) (0.41 and 0.43 for two experiments with IAP1R) and Jan-Orn et al. (1976) (0.45 for lines from NP3BR).

All heritability values presented for Experiment II in Table 13 were estimated by using variance components or parent-offspring regression. Realized heritability, however, was calculated on an individual-plant basis from the 100-seed weight data of Experiment I (Table 9). The estimate of realized heritability was 0.14 ± 0.08. This represents only 40% of the individual-plant heritability estimated for the C0 of Experiment II (0.35, Table 13). The low realized heritability may indicate (1) the estimates of σ^2_g from Experiment II may be inflated, (2) σ^2_D played a larger role in σ^2_G for this trait than I had reasoned, because I assumed that 100-seed weight was controlled primarily by σ^2_A, and (3) the actual σ^2_{ph} was greater than the value that I calculated for Experiment II.

Difficulties in estimating $\sigma^2_{S_1}$ have been cited in other investigations with sorghum. Jan-Orn et al. (1976) found that the ratio of σ^2_{A*}/σ^2_A was less than one for all the traits they studied (where $\sigma^2_{S_1} = \sigma^2_{A*} + \frac{1}{4}\sigma^2_D$ and $\sigma^2_{HS} = \frac{1}{4}\sigma^2_A$). They concluded that $\sigma^2_{S_1}$ was relatively low to σ^2_A because (1) σ^2_{A*} was less than σ^2_A when frequencies of favorable alleles were less than 0.5 and dominance variance and/or epistasis were

important, or (2) σ_A^2 was overestimated as a result of assortative mating. Similarly, Lothrop (1983) concluded that the unusual ratios of $\sigma_A^2/\sigma_{S_1}^2$ that he calculated for IAP1R resulted from overestimations of σ_A^2 and underestimations of $\sigma_{S_1}^2$. Both authors agree that $\sigma_{S_1}^2$ tends to be underestimated. If this is also true in IAP3BR(M), then the high heritability values probably are the result of underestimated values of σ_{ph}^2.

If the estimates of σ_{ph}^2 and $\sigma_{S_1}^2$ are in fact accurate, then the differences in realized and calculated heritability may be a result of inbreeding effects associated with advancing cycles. The unit of sampling also could be a factor, because the realized heritability calculation was based on data from HS bulks while the variance component and parent-offspring regression heritabilities were based on data from S_1 families. In any case, the overestimation of heritability would cause an overestimation of gains from mass selection, which in turn would be reflected in realized gains that are less than the estimated gains.

Expected gains from selection for 100-seed weight were calculated by using the methods for S_1 family testing (3 years/cycle) and for gridded mass selection (1 year/cycle). Ross et al. (1976) indicated that mass selection in sorghum should be very effective for highly heritable traits. Jan-Orn et al. (1976) advocated its use for plant height and maturity in sorghum, and more recently, Lothrop (1983) concluded from

studies with IAP1R that mass selection for 100-seed weight would be effective.

Gains/year by using gridded mass selection for 100-seed weight in IAP3BR(M) were estimated at 4.2% of the mean from the C0 data and 4.3% for the C4 (Table 15). Although there was a small decrease in the estimate of σ_g^2 (Table 12) for 100-seed weight between the C0 and C4, the percentage gain was nearly the same, perhaps a result of an offsetting small increase in heritability on an individual-plant basis (Table 13). These gains are similar to those reported for mass selection by Lothrop (1983) from two experiments with IAP1R(M)C3 (5.1 and 4.7%/year). However, they are substantially less than the value reported by Jan-Orn et al. (1976), who calculated a gain of 14.6%/year from experiments involving mass selection in lines from the population NP3R.

S_1 family selection generally is used for traits that have a low heritability or when large genotype by environment interactions seem likely. Lothrop (1983) reported gains from S_1 selection for 100-seed weight of 3.7 and 4.2% of the mean/year for two experiments with the population IAP1R. Jan-Orn et al. (1976) estimated a strikingly higher gain of 23.9%/year for 100-seed weight. Estimated gains in 100-seed weight by using S_1 family testing in IAP3BR(M) were 4.6%/year from the C0 data and 3.7%/year in C4 (Table 14). These values are much lower than the estimates by Jan-Orn et al. (1976) and

very close to those presented by Lothrop (1983). The decrease in rate of gain between the C0 and C4 when using S_1 family selection for 100-seed weight could be due to (1) an increase in the mean 100-seed weight in C4 (from 2.61 in C0 to 2.86, Table 11), (2) a smaller heritability value in the C4 (0.85 vs 0.90 in C0, Table 13), and (3) a decreased genetic variance for 100-seed weight in C4 (from 7.23 in C0 to 5.90, Table 12).

Gridded mass selection does not require large amounts of land and labor, it is simple to conduct, and it requires no yield testing. Because of the high heritability for 100-seed weight (Table 13) and the advantages just cited, mass selection seems the preferred method for improving seed size. S_1 family selection may be of benefit in future cycles of selection in IAP3BR(M), however, if the tendency for increased genotype x environment variance that was displayed between the C0 and C4 continues (Table 12). Continued mass selection for 100-seed weight should produce gains comparable to those observed in my experiments.

My results show clearly that selection through four cycles for 100-seed weight has been successful in IAP3BR(M), and they indicate that gridded mass selection should continue to produce increases in seed size. Plant breeders must be cotnizant as well of changes that may occur in related agronomic traits. Practically, the associated traits of

greatest concern would include grain yield and the other primary components of yield: seeds/panicle and panicles/plant.

100-seed weight was correlated significantly with grain yield in the C0 (Table 16), but in the C4, the coefficient was markedly smaller and the correlation was not significant (Table 17). Frey and Huang (1969) found a curvilinear response of 100-seed weight with grain yield in oats. They stated that correlations between these traits in different populations could be positive, negative, or zero depending on the range in 100-seed weight that was expressed by the genotypes tested. If this relationship is applicable to sorghums, it may be that the range and mean for 100-seed weight in the C0 of IAP3BR were sufficiently low to show appreciable correlation with grain yield ($r = 0.33$). But, after four cycles of selection, 100-seed weight may have reached an "optimum" level in relation to the total use of metabolites for grain production, yet the maximum in seed-size potential has not yet been reached. With those constraints relative to the means and ranges in the C4, the correlation of seed size and yield was very small and not significant ($r = 0.06$).

Support for this contention is provided by the linear and quadratic effects for grain yield exhibited by the four cycles of HS bulks (Tables 6 and 7). The highest yield among the HS bulks was recorded in C3, with the C2 and C4 yielding significantly less. If there is a definite curvilinear

response for yield, increasing 100-seed weights beyond the level expressed in C4 could result in a negative correlation between grain yield and 100-seed weight. Malm (1968) reported positive correlations of 0.29 and 0.67 between these traits in a 2-year study involving large-seeded exotic parents, and concluded that increases in seed size generally should be accompanied by higher grain yield. My results suggest that Malm's conclusion may only be valid until an "optimum" seed size is reached. My findings are more in keeping with those of Leng (1963) who found that highest grain yields in maize were associated with hybrids that had medium to medium-high 100-kernel weights.

The large negative correlations between 100-seed weight and seeds/panicle in both the C0 and C4 of IAP3BR (Tables 16 and 17) are in harmony with those found in previous investigations with lines from random-mating sorghum populations (Lothrop, 1983; Jan-Orn et al., 1976). Quinby and Schertz (1970) also found a strong inverse relationship between these two traits in studies involving inbred lines and hybrids and suggested that improvement of both traits simultaneously would be difficult.

The moderate correlation of 100-seed weight with panicles/plant ($r = 0.47$) in the C4 of IAP3BR contrasts with the small, nonsignificant correlation in the C0 ($r = 0.18$). A consideration of the sequential development of plant characters

associated with grain yield may have bearing on these observations. Eastin (1972) defined three growth stages in sorghum which span the period of development for panicles/plant (GS1), seeds/panicle (GS2), and 100-seed weight (GS3). It seems reasonable to expect that 100-seed weight should be most highly correlated with the trait that is closest to it in the sequence of development, i.e., seeds/panicle, and less so with panicles/plant. Further, it seems the correlation between seeds/panicle and 100-seed weight should remain strong over several cycles of selection (-0.72 in C0 and -0.78 in C4) of IAP3BR(M). But, as mean 100-seed weight of the population increased and moved towards an extreme, the correlation between 100-seed weight and the more distant trait in terms of sequential development, panicles/plant, increased (0.18 in C0 to 0.47 in C4).

This reasoning can be extended further from the standpoint of grain yield. In the C0 of IAP3BR, grain yield was correlated significantly with 100-seed weight, but not so with seeds/panicle or panicles/plant. The coefficients for yield with the three primary components are quite similar (0.33, 0.17, and 0.27), and the population could be considered in equilibrium with respect to impact of the yield components. If one selected for heavy 100-seed weight and increased it to an "optimum", but not maximum, level, the equilibrium would be disturbed. 100-seed weight might no

longer be correlated appreciably with grain yield, but compensatory effects could increase the correlations for grain yield with seeds/panicle and/or panicles/plant to significant levels. This reasoning was, in fact, borne out as shown by correlations for the C4 in Table 17. The means for the C0 and C4 in Table 11 also support this rationale. Increases in 100-seed weight (from 2.61 to 2.86 g/100 seeds) were accompanied by decreases in seeds/panicle (from 1423 to 1224) and panicles/plant (from 1.4 to 1.3). Rasmusson and Cannell (1970) studied interactions among yield components in barley and hypothesized that, because seed size is the last primary component to develop, its level of expression should not produce compensatory effects among the other yield components. My results with sorghum are not in agreement with that hypothesis.

Despite the stabilizing effects of compensation among yield components, selection to improve grain yield can be effective. Knott and Talukdar (1971) found that compensation among yield components in wheat was not complete, and they were able to increase grain yields appreciably. This seems true for the sorghum population IAP3BR(M) as well, because none of the correlations approach r = 1.00 and not many are beyond r = 0.70 (Tables 16 and 17). Additionally, there is ample genetic variation among genotypes in the population for all traits (Table 10).

Beil and Atkins (1967) and Jan-Orn et al. (1976) found that variations in grain yield among sorghum genotypes were attributable largely to effects of seeds/panicle and to a lesser extent to differences in 100-seed weight. Most investigations with grain yield in sorghum rank the primary components of yield in order of importance as seeds/panicle, then 100-seed weight, and lastly, panicles/plant. If a sorghum breeder desires to improve the contribution of yield components, my results from the C0 of IAP3BR indicated that direct selection for grain yield per se would provide small but positive gains in all components (Table 18). Estimates based on the C4 data show that no change would be expected in 100-seed weight, but that good gains in seeds/panicle and panicles/plant would be expected when selecting directly for grain yield.

If the primary goal of selection is to increase 100-seed weight, direct selection for that trait would result in the best gains, according to either the C0 or C4 data in Table 18. Selection for 100-seed weight likely could serve quite well as a means for indirect selection for yield improvement in sorghum. In the C0 of my experiments, correlated response of grain yield to selection for 100-seed weight was estimated at 26% (Table 18). Eckebil et al. (1977) likewise estimated noteworthy correlated responses of 49, 52, and 29% in grain yield when selection was for 100-seed weight in the sorghum

populations NP3R, NP5R, and NP7BR, respectively. Lothrop (1983) estimated a 21% gain in grain yield in one experiment and a -17% response for yield in another when selection was for heavy 100-seed weight. Both of his experiments were with the population IAP1R(C3), but one experiment was conducted only at Ames and the other was carried out at Ames and Castana, Iowa. His results indicated that correlated responses estimated from data obtained at one location may not prove out well when evaluations are made over several environments. In my studies with IAP3BR(M), the gain in grain yield when selection is for 100-seed weight was estimated at 0% in the C4 (Table 18), suggesting that selection for 100-seed weight beyond that cycle would not increase grain yield.

It appears that 100-seed weight in IAP3BR has reached an "optimum" level in the C4 if improvement of grain yield is the primary objective, and it may be desirable to change the selection procedure at this point. A similar situation exists in sunflowers. Russian plant breeders increased oil production, a trait primarily under additive gene control, by direct selection for increased oil content in open-pollinated varieties (Alexander, 1963). However, Putt (1966) suggested that sunflower growers should use synthetic varieties or hybrids to take advantage of the large amount of nonadditive gene action present for grain yield. Therefore, selection was carried out first for higher oil content (utilizing the

additive gene action) until a desirable or "optimum" level was reached. At that stage, the strategy was changed and selection was directed toward higher grain yield (utilizing nonadditive gene action). Oil content should be fixed at a high level while the plant breeder then capitalizes on non-additive gene effects to achieve gains in grain yield.

A similar system may serve for the improvement of IAP3BR (M). Seed size is controlled primarily by additive gene action and it seems that size may have reached an "optimum" level in association with grain yield improvement. It may be beneficial to change the selection program to take advantage of hybrid vigor for grain yield if good genetic variability for yield exists and nonadditive gene action is important in its expression.

Mean grain yield demonstrated a curvilinear response over cycles when HS bulks were analyzed in Experiment I. The highest grain yields were associated with C3. The S_1 bulks did not show a definitive pattern of response for yield over the four cycles. In Experiment II, a significant decrease was noted for grain yield between S_1 families of the C0 and those of the C4 (Table 10). The large ranges in Table 11 indicate that good variability exists between the high and low genotypes and the genetic variance for yield increased significantly from C0 to C4 (Table 12). Mean yield of the C0, however, may have been overestimated. The C0 seed was

produced under adverse conditions in 1977, and an appreciable number of the plots from this seed were short and required corrections for grain yield. It seems there is a tendency to over-correct in adjusting data for short plots or sparse stands, and thereby bias those values upward from their true value. In addition, yields were obtained from fewer S_1 families in the C0, 49 vs 58 for the C4. These factors also may have contributed to an underestimation of σ^2_g. Nevertheless, the S_1 families from IAP3BR(M) displayed good variability for grain yield. Grain yield was the only trait that showed significant inbreeding depression (-29.6%) in my experiments. This value is substantially greater than the -13.9% reported by Lothrop (1983) from studies with the population IAP1R. Both estimates suggest that nonadditive gene action exerts considerable impact on the expression of grain yield in sorghum.

Estimates of heritability for grain yield on a progeny-mean basis for the C0 (0.58) and C4 (0.77) were similar to those determined by Lothrop (1983) (0.85 and 0.74) in two experiments involving C3 lines from IAP1R. They also are close to the values reported by Eckebil et al. (1977) (0.74, 0.75, and 0187) for three populations evaluated in Nebraska. Heritabilities in my experiments for grain yield on an individual-plant basis were -0.12 for the C0 and 0.03 for the C4. These estimates are smaller than those presented by Lothrop

(1983) (0.06 and 0.13 for two experiments with IAP1R) and Jan-Orn et al. (1976) (0.09 for grain yield in NP3R).

A perusal of the estimated gains from gridded mass selection and S_1 family selection for grain yield (Tables 14 and 15) indicates that gridded mass selection would produce very little gain (based on the C4 data) or no gain (based on the C0 data). S_1 family selection seems clearly the better choice for increasing grain yield. Estimated gains of 1.8%/year should be realized according to the C0 calculations, and 3.6% gain/year was indicated from the C4 data. My experiments did not provide data for comparisons with half-sib family testing. But Lothrop (1983) and Jan-Orn et al. (1976) found that S_1 family selection produced the largest gains/year for grain yield when compared with half-sib family testing and mass selection. The advantage of S_1 family testing over mass selection in IAP3BR(M) seems a function of low heritability for grain yield and the need for testing at several locations because of large g x e interaction.

Although I was interested primarily in the evaluation of interrelationships between 100-seed weight and grain yield in IAP3BR(M), examination of the variability for seeds/panicle and panicles/plant also was an objective of my studies. The results from Experiment II indicated that selection for 100-seed weight resulted in significant decreases in the means for seeds/panicle (1423 to 1224) and panicles/plant (1.4 to

1.3) (Tables 10 and 11). However, large ranges of expression were evident for each of these traits among the C0 and C4 S_1 families. Interestingly, the estimates of σ_g^2 in the two cycles were similar for seeds/panicle, but the estimate for panicles/plant was much smaller in the C4 (Table 12). The selection of large panicles in each isolation block for advancing the population could have resulted in the inadvertent choice of genotypes with a low number of panicles/plant and a decrease in the variance for that character.

Heritabilities on a progeny-mean basis for seeds/panicle (0.79 in C0 and 0.84 in C4) were very similar to those calculated by Lothrop (1983) (0.79 and 0.80 in two experiments with C3 lines of IAP1R). Estimates of heritability for panicles/plant in my studies were 0.64 in C0 and 0.19 in C4. Both values are lower than the estimates of 0.66 and 0.77 presented by Lothrop (1983).

Adequate genetic variability and high heritability for seeds/panicle and panicles/plant should make these traits suitable for indirect selection for grain yield. Estimates of correlated response, based on both the C0 and C4 data, indicated that panicles/plant would give the better indirect gain in grain yield (Table 18). This relationship contradicts the findings of Lothrop (1983) who estimated that greatest indirect gains in yield would be produced by selection for seeds/panicle, followed by panicles/plant, and

finally, 100-seed weight. These differences in correlated response may be due to the impact of the large-seeded germplasm that was infused into IAP3BR(M) that was not present among the parents of IAP1R.

If the primary objective of a selection program is to increase grain yield and/or 100-seed weight in acceptable agronomic types, adequate variability must be available not only for those traits but also for maturity, plant height, and panicle type. In Experiment I, only days to midbloom displayed a significant linear response to selection for seed size, when HS bulks were the unit of evaluation (Table 6). Character means showed an increase across cycles for days to midbloom, but the changes for plant height did not display a definitive pattern of response (Table 7). In Experiment II, mean days to midbloom increased from the C0 to C4, as did plant height and openness of panicles. High and low genotype values for these characters indicate that genotypes with marked diversity of expression could be isolated from the population (Table 11).

The estimates of variance components in Table 12 indicate that σ_g^2 for days to midbloom, plant height, and panicle type has increased from the C0 to C4. Latent variability for these traits apparently has been released as a result of recombination. Heritability estimates (Table 13) were high for days to midbloom, plant height, and panicle type in both the C0 and C4.

Inbreeding depression was determined to be high for plant height (-22.7%) and low (3.0%) for days to midbloom. The large value for plant height indicates that nonadditive gene action plays a prominent role in the determination of height, or that its expression is under qualitative gene control.

Estimates for the heritability of days to midbloom on a progeny-mean basis (Table 13, 0.82 in C0 and 0.91 in C4) were very similar to the value calculated by Jan-Orn et al. (1976) (0.88 for NP3R). But for plant height, my estimates of 0.83 in C0 and 0.85 in C4 were somewhat higher than the value of 0.71 determined from S_1 families of NP3R. The high heritabilities indicate that adjustments for either of these traits in IAP3BR may be relatively easy to accomplish.

Days to midbloom showed poor correlation with grain yield and 100-seed weight (Tables 16 and 17). The low correlation of midbloom with 100-seed weight suggests that the changes in maturity that occurred over cycles resulted from adjustments of the population to seasonal fluctuations in the growing conditions at Ames, and were not a result of the selection for large seed.

Selection for large seed tended to increase mean plant height (Tables 7 and 11). The C0 mean of 154.3 cm in Experiment II rose to 160.7 cm in C4. This increase is not surprising because the phenotypic correlation between these characters was 0.51 in the C0 and the genetic correlation was 0.69

(Table 16). Both types of correlations were appreciably smaller in the C4 (0.25 and 0.35, respectively). The C4 correlations are smaller than those reported by Lothrop (1983) (r = 0.26) and Jan-Orn et al. (1976) (r = 0.39). The reduced correlation between these traits from the C0 to C4 may indicate that an "optimum" plant height:100-seed weight ratio has been reached in the C4.

Phenotypic correlations of plant height with grain yield in IAP3BR (0.44 in C0 and 0.47 in C4) are larger than those estimated by Jan-Orn et al. (1976) (0.29 in NP3R) and Lothrop (1983) (0.41 in IAP1R). My coefficients more nearly support the work of Casady (1965) and Campbell and Casady (1969). Their results indicated a strong relationship between grain yield and plant height and suggested that selection for high yielding combine height sorghums would be difficult. The correlation of grain yield with panicle type was near zero (0.04) in the C0, but it increased to 0.34 in the C4. The stronger relationship in the C4 suggests some tendency for high grain yield to be associated with plant types that have an open panicle.

Genetic correlations between seemingly unrelated traits are most likely due to pleiotropy, because it seems justifiable to assume that a random-mating population such as IAP3BR(M) is at linkage equilibrium. The genetic correlations presented in Tables 16 and 17 generally are in agreement with

the phenotypic correlations. Several genetic correlations, however, were distinctly greater in magnitude than their phenotypic counterparts. The most notable of these were grain yield with plant height (0.94 vs 0.44 in C0, and 0.73 vs 0.47 in C4), and panicles/plant with days to midbloom (-1.05 vs -0.39 in C0, and -0.95 vs -0.51 in the C4).

Falconer (1981) demonstrated that the association observed between two characters (phenotypic correlation) is a combination of both genetic and environmental correlations. In the case of grain yield with plant height, the high genetic correlation may be offset by a negative environmental correlation. The negative environmental correlation would indicate environments favorable for grain yield would be detrimental to plant height or vice versa. In the case of panicles/plant with days to midbloom, positive environmental correlations may be offsetting the large negative genetic correlations. The positive environmental correlations indicate that the environments favorable for panicle development are also favorable for increasing days to midbloom.

The estimates of correlated response to S_1 family selection (Table 18) for either grain yield or 100-seed weight indicate that only small changes in days to midbloom would occur. Less than 10% of the gain that could be obtained by direct selection for midbloom date was estimated from the C0 and C4 data. The correlated responses for plant height,

however, suggest that considerable increase in plant height would accompany selection for either grain yield or 100-seed weight. Estimates of response from the C4 data indicate that selection for grain yield would have an appreciable tendency to be reflected in more open-panicle types in the population.

SUMMARY

Two experiments were conducted with genotypes from the sorghum random-mating population IAP3BR(M) to elucidate the population response to four cycles of gridded mass selection for heavy 100-seed weight (large seed). Entries in Experiment I consisted of composites of seed from fertile panicles (S_1 bulks) from recurrent selection cycles 0, 2, 3, and 4, and composites of seed from male-sterile panicles (half-sib bulks) from cycles 1, 2, 3, and 4. Experiment II evaluated 60 S_1 families chosen randomly from each of the initial (C0) and fourth (C4) cycles of the population.

The entries in both experiments were evaluated in replicated tests at Ames, Beaconsfield, and Sutherland, Iowa, in 1982 and 1983. 100-seed weight was evaluated at all locations both years. Grain yield, seeds/panicle and panicles/plant were evaluated at all locations in 1982 and at Ames and Beaconsfield in 1983. Plant height and days to midbloom were evaluated at Ames both years, and panicle type was evaluated at all locations in 1983.

Gridded mass selection for 100-seed weight was effective in increasing 100-seed weight from the C0 to the C4. The results for grain yield did not display a consistent pattern of change over cycles. Mean yield in Experiment I showed a curvilinear response over cycles, with an overall increase from C0 to C4 for HS bulks. Changes for S_1 bulks lacked a

definite pattern and showed an overall decrease between C0 and C4. Experiment II showed a decrease in mean grain yield from the C0 to C4. Decreases from the C0 to C4 were noted in both experiments in the means for seeds/panicle and panicles/plant while increases were noted for days to midbloom, plant height, and openness of panicle.

Mean 100-seed weights for the S_1 families in Experiment II were 2.61 g in the C0 (range 1.21 to 4.22 g) and 2.86 g in the C4 (range 1.44 to 4.44 g). Grain yields of the S_1s averaged 54.2 and 50.3 q/ha for the C0 and C4, respectively. A wide range in yield was displayed, with genotype means from 15.0 to 106.2 q/ha in the C0 and 14.1 to 99.9 q/ha in the C4.

Estimates of inbreeding depression determined from the S_1 and HS family bulk means of Experiment I were significant ($P<0.05$) only for grain yield (-29.6%), indicating that non-additive gene action contributed appreciably to the expression of grain yield. Inbreeding was not significant beyond the 0.05 probability level for 100-seed weight (-14.0%), seeds/panicle (-10.2%) and plant height (-22.7%).

Estimates of genotypic variance for 100-seed weight in Experiment II decreased from 7.23 in C0 to 5.90 in C4, but the difference did not exceed $P<0.05$. Significant increases in genotypic variance from the C0 to C4 were noted for grain yield, days to midbloom and openness of panicle, indicating

that the selection for seed size over four cycles had resulted in the release of latent variability for these characters. Variance estimates for panicles/plant indicated that a significant and pronounced decrease in genotypic variability occurred between the C0 and C4.

Genotype x environment variance estimates for S_1 families (Experiment II) increased significantly ($P<0.01$) from the C0 to C4 for 100-seed weight, but decreased significantly for seeds/panicle. This seems to indicate that lines derived from the C4 may be less stable across environments than those from the initial population for 100-seed weight, but more stable for seeds/panicle. The estimate of σ^2_{ge} for days to midbloom also was larger in the C4, but the values for grain yield and the other characters measured did not differ significantly between the C0 and C4.

Heritability of 100-seed weight, based on the progeny means of S_1 families, decreased slightly from the C0 to C4 (0.90 vs 0.85) in Experiment II. Increases in heritability between these cycles were noted for grain yield (0.58 vs 0.77) and seeds/panicle (0.79 vs 0.84). Panicles/plant showed a marked decrease in heritability between the cycles (0.64 in C0 to 0.19 in C4). Days to midbloom, plant height and panicle type all showed high heritabilities, with very similar estimates in the C0 and C4. Heritability estimates for 100-seed weight on an individual-plant basis were 0.35 in the C0 and

0.39 in the C4. Both values were greater than the estimate of realized heritability (0.14) determined in Experiment I by regression of cycle means on the cumulative selection index.

Estimated gains from gridded mass selection for heavy 100-seed weight were 4.2 and 4.3% of the mean per year, based on data from the C0 and C4 of Experiment II, respectively. Gains from S_1 family selection for 100-seed weight were estimated at 4.6 and 3.7% of the mean per year for the C0 and C4, respectively. S_1 family selection for grain yield should be effective for improving grain yield, as indicated by estimated gains of 1.8 and 3.6% of the mean per year for the C0 and C4, respectively. The estimated gains from gridded mass selection for grain yield, however, indicated that it would not be useful for improving grain yield. Estimates based on the C4 data indicated a gain of 0.4% of the mean per year, while a value of -0.8% of the mean per year was obtained using C0 data. Smaller labor requirements and lower costs for gridded mass selection, together with a higher rate of gain in the C4, suggest that gridded mass selection would be the preferable method to use for continued improvement of 100-seed weight in IAP3BR.

Phenotypic correlations determined in Experiment II between 100-seed weight and grain yield decreased from $r = 0.33$ in the C0 to $r = 0.06$ in C4. The coefficient in the C0 indicates that modest improvement in grain yield should

accompany selection for large seed. In C4, the r value indicates that grain yield should be neither enhanced nor depressed by selection for heavy seed. Strong negative correlations between 100-seed weight and seeds/panicle were exhibited in both cycles (-0.72 in the C0 and -0.78 in C4). This association imparts a pronounced dampering effect on the improvement of grain yield through simultaneous selection for both components of yield.

The correlation between 100-seed weight and panicles/plant increased from the C0 ($r = 0.18$) to the C4 ($r = 0.47$), while the correlation between plant height and 100-seed weight decreased between these cycles (0.51 vs 0.25). The low correlation in C4 between plant height and 100-seed weight suggests that there should be little difficulty in selecting a diversity of height genotypes that have large seed. Correlations of grain yield with seeds/panicle and with panicles/plant changed from 0.17 and 0.27, respectively, in the C0 to 0.40 and 0.46, respectively, in the C4. Genetic correlations among most characters were similar in direction and magnitude to the phenotypic correlations, but for several traits, the genetic correlations were higher.

Correlated responses to selection determined in Experiment II indicated that selection for 100-seed weight in the C0 would be effective for increasing grain yield as well. But the estimates of response calculated from the C4 data

showed no gain in grain yield in consort with selection for large seed. For recurrent selection beyond the C4, it seems advisable to change the breeding strategy for IAP3BR from gridded mass selection for 100-seed weight to S_1 family testing for grain yield to realize continued improvement of grain yield in the population.

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APPENDIX

Table A1. Means and variances for grain yield and 100-seed weight of randomly chosen fertile plants from which the S_1 families tested in Experiment II were derived, as grown in the 1977 (C0) and 1981 (C4) isolation plantings of IAP3BR(M)

Experiment	Plant type	Grain yield		100-seed weight	
		Mean	Variance	Mean	Variance
		g			
		C0			
60[a]	Fertile	76.6 ± 1.0	58.66	2.62 ± 0.06	0.2098
		C4			
60	Fertile	97.7 ± 2.1	257.26	3.51 ± 0.07	0.2849

[a]Grain yield in C0 is based on 59 fertile plants due to loss of one entry.

Table A2. Individual-year means, for half-sib bulk entries, for characters measured in Experiment I, Ames, Beaconsfield, and Sutherland, 1982 and 1983

	Ames		Beaconsfield		Sutherland	
Character	1982	1983	1982	1983	1982	1983
Grain yield (q/ha)	77.3±1.9	91.2±3.0	51.5±2.5	52.3±1.1	36.1±1.3	-
100-seed weight (g)	3.47±0.06	3.15±0.10	3.18±0.11	2.94±0.08	2.36±0.07	2.82±0.06
Seeds/ panicle	1007±41	1417±80	1118±52	1689±56	1179±61	-
Panicles/ plant	1.8±0.06	2.2±0.10	1.2±0.04	1.1±0.02	1.1±0.04	-
Days to midbloom	67±0.4	67±0.5	-	-	-	-
Plant height (cm)	176±2.5	176±4.0	-	-	-	-

Table A3. Individual-year means for S_1 bulk entries, for characters measured in Experiment I, Ames, Beaconsfield, and Sutherland, 1982 and 1983

	Ames		Beaconsfield		Sutherland	
Character	1982	1983	1982	1983	1982	1983
Grain yield (q/ha)	60.9±1.0	79.2±3.5	50.4±2.0	44.9±1.5	29.3±0.8	-
100-seed weight (g)	3.01±0.09	3.30±0.12	2.87±0.08	2.76±0.07	2.15±0.07	2.60±0.06
Seeds/ panicle	1063±34	1262±53	1170±59	1521±55	1057±50	-
Panicles/ plant	1.5±0.02	2.0±0.07	1.3±0.07	1.1±0.02	1.1±0.05	-
Days to midbloom	68±0.5	68±0.3	-	-	-	-
Plant height (cm)	159±2.2	153±3.3	-	-	-	-

Table A4. Mean squares from the ANOVA for characters measured in Experiment I, Ames, 1982

Source of variation[a]	df	Mean squares					
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	Days to midbloom	Plant height
		(÷10)	(x10)	(÷100)	(x10)		(÷10)
Replications (rep)	3	0.11	10.8	4.11	4.7	1.36	0.57
S_1 vs HS	1	21.41**	163.8**	2.50	50.0**	1.53	23.46**
HS (L)	1	1.25	1.9	1.11	0.6	13.61*	0.42
HS (Q)	1	2.35**	5.8	9.38*	1.6	3.06	6.00**
HS (C)	1	0.35	0.5	3.01	10.5	4.51	4.23**
S_1 (L)	1	0.30	44.9*	0.30	0.1	14.46*	3.68**
S_1 (Q)	1	0.13	3.5	1.13	2.0	0.27	2.88**
S_1 (C)	1	0.20	8.8	0.31	0.1	0.51	0.74
Error	21	0.31	8.2	1.93	2.9	2.65	0.34

[a] S_1 = S_1 family bulk; HS = half-sib family bulk; (L) = linear effects; (Q) = quadratic effects; (C) = cubic effects; as used in this and all subsequent tables.

*,**Indicate significance beyond the 0.05 and 0.01 probability levels, respectively, in this and all subsequent tables.

Table A5. Mean squares from the ANOVA for characters measured in Experiment I, Ames, 1983

Source of variation	df[a]	Mean squares: Grain yield (÷10)	100-seed weight (x10)	Seeds/ panicle (÷100)	Panicles/ plant (x10)	Days to midbloom	Plant height (÷10)
Replications (rep)	3	0.53	21.8	5.78	4.6	0.86	5.70**
S_1 vs HS	1	12.84**	17.9	13.94	38.0	5.28	43.24**
HS (L)	1	1.64	12.6	9.57	23.5	20.00**	12.80**
HS (Q)	1	4.44	38.4	6.13	17.1	6.25	0.64
HS (C)	1	0.69	16.7	3.66	1.1	0.00	0.45
S_1 (L)	1	2.54	25.8	7.97	10.7	0.00	5.92*
S_1 (Q)	1	0.14	46.4	2.72	0.6	1.87	5.57*
S_1 (C)	1	0.01	67.5*	2.23	5.3	9.31	1.04
Error	21	1.43	13.7	5.59	10.5	2.51	0.94

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 6 less degrees of freedom for error.

Table A6. Mean squares from the ANOVA for characters measured in Experiment I, Beaconsfield, 1982

Source of variation	df	Mean squares			
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant
		(÷10)	(x10)	(÷100)	(x10)
Replications (rep)	3	2.22*	4.4	4.04	23.1**
S_1 vs HS	1	0.18	74.4*	2.14	0.8
HS (L)	1	2.10	134.4**	0.45	0.6
HS (Q)	1	0.01	0.1	1.52	0.1
HS (C)	1	2.03	41.9	25.62*	1.5
S_1 (L)	1	0.48	14.6	2.14	0.3
S_1 (Q)	1	0.61	3.0	9.46	15.0*
S_1 (C)	1	0.02	5.2	0.34	3.3
Error	21	0.60	12.0	4.62	3.4

Table A7. Mean squares from the ANOVA for characters measured in Experiment I, Beaconsfield, 1983

Source of variation	df	Mean squares			
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant
		(÷10)	(x10)	(÷100)	(x10)
Replications (rep)	3	0.14	9.3	0.53	0.9
S_1 vs HS	1	4.48**	26.5	22.70	0.3
HS (L)	1	0.22	11.6	0.20	0.1
HS (Q)	1	0.32	5.6	1.66	0.1
HS (C)	1	0.08	20.5	19.64	0.0
S_1 (L)	1	0.00	0.5	0.14	1.0
S_1 (Q)	1	0.22	0.2	0.04	0.5
S_1 (C)	1	0.02	2.4	2.80	0.4
Error	21	0.32	9.7	5.70	0.5

Table A8. Mean squares from the ANOVA for characters measured in Experiment I, Sutherland, 1982 and 1983

Source of variation	df[a]	Mean squares				
		1982				1983
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	100-seed weight
		(÷10)	(x10)	(÷100)	(x10)	(x10)
Replications (rep)	3	0.68**	8.2	5.97	5.8	7.4
S_1 vs HS	1	3.62**	38.1*	12.65	0.3	39.2*
HS (L)	1	0.03	39.2*	19.88*	6.5	13.9
HS (Q)	1	0.01	3.4	3.42	0.5	0.5
HS (C)	1	0.17	24.2	6.26	0.9	1.8
S_1 (L)	1	0.12	4.4	2.04	2.3	12.6
S_1 (Q)	1	0.07	4.2	1.88	4.1	3.9
S_1 (C)	1	0.03	0.5	10.03	13.1*	0.1
Error	21	0.11	6.8	3.81	3.0	6.4

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 1 less degree of freedom for error.

Table A9. Individual-year means for all entries for characters measured in Experiment II, Ames, Beaconsfield, and Sutherland, 1982 and 1983

	Ames		Beaconsfield		Sutherland	
Character	1982	1983	1982	1983	1982	1983
Grain yield (q/ha)	66.8±0.7	70.7±0.7	44.9±0.7	47.1±0.5	32.5±0.5	-
100-seed weight (g)	3.01±0.03	3.11±0.03	2.80±0.03	2.72±0.03	2.21±0.03	2.57±0.03
Seeds/ panicle	1135±17	1403±27	1242±24	1655±25	1175±17	-
Panicles/ plant	1.6±0.02	1.8±0.02	1.1±0.01	1.1±0.01	1.1±0.01	-
Days to midbloom	68±0.2	69±0.2	-	-	-	-
Plant height (cm)	159±1.4	157±1.4	-	-	-	-
Panicle type	-	2.7±0.06	-	2.5±0.06	-	2.9±0.05

Table A10. Individual-year means, for CO entries, for characters measured in Experiment II, Ames, Beaconsfield, and Sutherland, 1982 and 1983

	Ames		Beaconsfield		Sutherland	
Character	1982	1983	1982	1983	1982	1983
Grain yield (q/ha)	68.2±1.0	71.6±1.1	47.6±1.0	49.4±0.8	34.8±0.6	-
100-seed weight (g)	2.81±0.04	2.97±0.04	2.71±0.04	2.61±0.04	2.14±0.03	2.42±0.03
Seeds/ panicle	1234±24	1521±43	1378±39	1780±43	1263±25	-
Panicles/ plant	1.6±0.02	1.8±0.04	1.1±0.02	1.2±0.02	1.1±0.02	-
Days to midbloom	67±0.2	68±0.2	-	-	-	-
Plant height (cm)	155±2.0	155±1.9	-	-	-	-
Panicle type	-	2.6±0.07	-	2.4±0.07	-	2.8±0.07

Table A11. Individual-year means for C4 entries, for characters measured in Experiment II, Ames, Beaconsfield, and Sutherland, 1982 and 1983

Character	Ames		Beaconsfield		Sutherland	
	1982	1983	1982	1983	1982	1983
Grain yield (q/ha)	65.5±1.0	70.0±1.0	42.9±0.9	45.5±0.6	30.5±0.7	-
100-seed weight (g)	3.22±0.04	3.25±0.04	2.89±0.04	2.83±0.03	2.27±0.04	2.73±0.04
Seeds/ panicle	1041±24	1306±30	1141±26	1568±27	1097±21	-
Panicles/ plant	1.6±0.02	1.8±0.03	1.1±0.02	1.1±0.01	1.0±0.01	-
Days to midbloom	69±0.2	70±0.3	-	-	-	-
Plant height (cm)	163±2.0	158±2.0	-	-	-	-
Panicle type	-	2.8±0.09	-	2.6±0.08	-	3.1±0.08

Table A12. Mean squares from the ANOVA for characters measured in Experiment II, Ames, 1982

Source of variation	df[a]	Mean squares: Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	Days to midbloom	Plant height
		(÷10)	(x10)	(÷100)	(x10)		(÷10)
Replications (rep)	1	9.39	17.55	6.22	0.00	27.34	11.31
Sets/rep	10	1.04	26.40	7.35	8.00	15.82	10.39
Genotypes/sets	114						
C0 vs C4/sets	6	1.97	178.31**	39.44**	10.00	45.85**	15.07**
C0/sets	54	1.51**	29.55**	8.90**	7.00**	6.12**	7.37**
C4/sets	54	1.44**	25.24**	6.70**	13.00**	20.71**	8.21**
Error							
C0vs C4	6	1.08	4.52	4.80	4.00	2.70	1.37
C0	54	0.49	8.96	3.74	3.00	1.09	1.56
C4	54	0.46	12.05	2.41	2.00	1.96	0.88

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 1 less degree of freedom for genotypes/sets and C0/sets; 8 less degrees of freedom for C0 error, and 4 less degrees of freedom for C4 error.

Table A13. Mean squares from the ANOVA for characters measured in Experiment II, Ames, 1983

Source of variation	df[a]	Mean squares: Grain yield (÷10)	100-seed weight (x10)	Seeds/ panicle (÷100)	Panicles/ plant (x10)	Days to midbloom	Plant height (÷10)	Panicle type
Replications (rep)	1	3.17	34.96	9.66	0.00	4.82	31.03	0.50
Sets/rep	10	0.71	30.84	14.15	8.00	4.16	4.89	1.23
Genotypes/sets	114							
C0 vs C4/sets	6	0.77	96.36*	38.19	4.00	27.28**	9.01*	0.86*
C0/sets	54	1.17	30.97**	17.07	12.00**	7.04**	6.88**	1.06**
C4/sets	54	1.12**	21.79**	12.29**	13.00**	19.33**	7.99**	1.17**
Error								
C0 vs C4	6	0.49	19.42	14.84	3.00	0.81	1.55	0.14
C0	54	0.68	11.04	9.55	5.00	1.75	1.18	0.23
C4	54	0.49	6.64	3.48	5.00	2.11	1.41	0.19

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 11 less degrees of freedom for genotypes/sets; 8 less degrees of freedom for C0/sets; 3 less degrees of freedom for C4/sets; 34 less degrees of freedom for C0 error; and 20 less degrees of freedom for C4 error.

Table A14. Mean squares from the ANOVA for characters measured in Experiment II, Beaconsfield, 1982

Source of variation	df[a]	Mean squares: Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant
		(÷10)	(x10)	(÷100)	(x10)
Replications (rep)	1	13.39	136.05	8.38	1.00
Sets/rep	10	2.07	37.82	18.97	6.00
Genotypes/sets	114				
C0 vs C4/sets	6	2.48	74.08**	49.94*	1.00
C0/sets	54	0.81*	20.30	14.33**	2.00
C4/sets	54	1.05**	22.76**	10.48**	4.00**
Error					
C0 vs C4	6	0.61	2.75	8.93	3.00
C0	54	0.43	13.69	5.30	2.00
C4	54	0.33	11.24	3.75	2.00

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 8 less degrees of freedom for genotypes/sets; 7 less degrees of freedom for C0/sets; 1 less degree of freedom for C4/sets; 31 less degrees of freedom for C0 error and 9 less degrees of freedom for C4 error.

Table A15. Mean squares from the ANOVA for characters measured in Experiment II, Beaconsfield, 1983

Source of variation	df[a]	Mean squares				
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	Panicle type
		(÷10)	(x10)	(÷100)	(x10)	
Replication (rep)	1	0.07	67.42	3.45	2.00	0.20
Sets/rep	10	0.52	18.25	10.02	3.00	0.29
Genotypes/sets	114					
C0 vs C4/sets	6	1.80**	58.52*	45.96*	8.00	0.80
C0/sets	54	0.46	26.61**	17.45	3.00**	1.11**
C4/sets	54	0.51	19.30**	10.33*	1.00	1.61**
Error						
C0 vs C4	6	0.21	8.07	5.78	4.00	0.40
C0	54	0.61	6.10	10.71	1.00	0.20
C4	54	0.35	8.10	5.52	1.00	0.14

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 14 less degrees of freedom for genotypes/sets; 13 less degrees of freedom for C0/sets; 1 less degree of freedom for C4/sets; 29 less degrees of freedom for C0 error; and 7 less degrees of freedom for C4 error.

Table A16. Mean squares from the ANOVA for characters measured in Experiment II, Sutherland, 1982 and 1983

Source of variation	df[a]	Mean squares					
		1982				1983	
		Grain yield	100-seed weight	Seeds/ panicle	Panicles/ plant	100-seed weight	Panicle type
		(÷10)	(x10)	(÷100)	(x10)	(x10)	
Replications (rep)	1	0.12	10.09	2.43	5.00	1.19	3.75
Sets/rep	10	0.57	24.38	5.43	5.00	33.62	0.78
Genotypes/sets	114						
C0 vs C4/sets	6	2.30**	23.60	33.32*	4.00	110.23**	1.49**
C0/sets	54	0.45**	22.69**	7.24	3.00	16.89**	0.84**
C4/sets	54	0.79**	34.37**	7.00*	3.00	24.09**	1.40**
Error							
C0 vs C4	6	0.22	9.83	4.14	1.00	4.47	0.11
C0	54	0.19	5.54	4.57	2.00	6.54	0.30
C4	54	0.22	6.93	3.73	2.00	6.55	0.12

[a]Because of missing values, the characters grain yield, seeds/panicle, and panicles/plant had 4 less degrees of freedom for genotypes/sets and C0 sets; 14 less degrees of freedom for C0 error; and 3 less degrees of freedom and C4 error.