# Population improvement in sorghum

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## Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is the fifth important cereal crop in the world after wheat, rice, maize and barley. Of late, it has emerged as 'fuel' crop in addition to its food, feed and fodder utilities. Sorghum is predominantly a self-pollinated crop and development of new varieties is a natural option for crop improvement. However, there is 5 to 15% outcrossing depending upon the nature of genotype and humidity (House 1985), which makes it possible to use population improvement and hybrid development methods to exploit the heterosis. Discovery of genetic male sterility (GMS) (Table 8) and cytoplasmic-nuclear male sterility (CMS) facilitated the application of recurrent selection procedures (population improvement) and hybrid cultivar development methods, respectively, in sorghum improvement programs.

Sorghum breeders have been successful in exploiting available vast genetic variability in sorghum by direct selection among landraces and/or by the use of conventional methods of handling segregating generations derived from carefully and deliberately effected crosses through pedigree and backcross breeding in the development of pure-line varieties and/or hybrid parents. These conventional breeding methods, used as a short-term strategy produce varieties with a relatively narrow genetic base, favor the accumulation of linkage blocks due to rapid fixation of genes, and limit recombination options because of continuous inbreeding. On the other hand, population improvement methods, besides offering greater opportunities for recombination to break linkages between desired and undesired traits, provides scope for increased utilization of biotic and abiotic stress resistant, but agronomically non-elite source germplasm lines. The population improvement provides long-term breeding strategy to derive diverse and broad genetic-based superior varieties/hybrid parents (Bola Nath 1982). Therefore, a comprehensive crop improvement strategy has to combine both short- and long-term programs for continuous improvement of economic traits.

## What is population improvement?

A population is a group of plants sharing a common gene pool. Population improvement includes (1) the development of broad genetic-based gene pools and (2) its improvement through recurrent selection methods. Recurrent selection was first suggested by Jenkins (1940) and named by Hull (1945). Recurrent selection methods are most suitable for the improvement of those traits that are inherited in a quantitative manner and the essential features of these methods are i) the improvement of the mean performance of the population by increasing the frequency of the genes that effect trait/traits under selection, ii) appearance of new combination of genotypes that never existed in the base population and iii) maintenance of genetic variability by recombination of superior genotypes for further and continuous improvement.

The recurrent selection methods require extensive hybridization, which is tedious to follow in sorghum owing to its inbreeding system. However, the discovery of genetic male-sterility (GMS) and the advent of various mating systems and reciprocal recurrent selection methods in exploiting additive (A) and A×A and other epistatic genetic variation (Comstock and Robinson 1952, Eberhart 1972), led many breeders to adopt population improvement methods in sorghum in the 1960s (Maunder 1972; Doggett 1972a). Several sources of genetic male sterility have been reported from both India and USA, and in all cases it was shown that a recessive allele in homozygous condition at a number of loci with alleles designated as $ms_{1,}$ $ms_{2,}$ $ms_{3,}$ $ms_{4,}$ $ms_{5,}$ $ms_{6}$, $ms_{7}$ and *al* confer male sterility (Table 8). Of these, only $ms_{3}$ and $ms_{7}$ alleles have been extensively used in population improvement as they are stable across locations and seasons (Reddy and Stenhouse 1994), although *al* (antherless) allele is also useful (House 1985).

## Development of random-mating populations

Populations can be developed for different purposes: for improving a single trait; for selecting several traits simultaneously; and for generating fertility restorer and non-restorer (maintainer) populations for deriving hybrid parents. Whatever the purpose, the development of a population involves three steps: (a) selection of component parents (b) introgression of a GMS gene, and (c) random mating among parents.

**Table 8. Genetic male sterility genes, their designated symbols and mechanism of sterility in sorghum. Source: Adapted from Rooney (2000).**

| Gene symbol | Mechanism | Reference |
|---|---|---|
| $ms_1$ | Normal pollen is dominant over aborted or empty pollen cells | Ayyangar and Ponnaiya (1937) |
| $ms_2$ | Normal pollen is dominant over aborted or empty pollen cells | Stephens (1937) |
| $ms_3$ | Normal pollen is dominant over aborted or empty pollen cells | Webster (1965) |
| $ms_4$ | Empty pollen cells | Ayyangar (1942) |
| $ms_5$ | Aborted pollen | Barabas (1962) |
| $ms_6$ | Micro-anthers without pollen | Barabas (1962) |
| $ms_7$ | Empty pollen cells | Andrews and Webster (1971) |
| al | Anther less stamens | Karper and Stephens (1936) |

## Population improvement methods

Once the broad genetic-based populations are developed, their genetic potential can be upgraded theoretically for any number of traits of interest through selection. Selection process is cyclic, with or without progeny testing and a recombination phase involving intercrossing among the selects. The process of selection and the intercrossing among the selects constitute one cycle and many such cycles are repeated and hence the whole process is referred to as recurrent selection. Various population improvement/selection methods have been developed and they could be classified based on the type of population (ie, intra-population and inter-population) and on the units of selection. In intra-population improvement, selection is practiced within a specific population for its improvement while in inter-population improvement; selection is based on the intercross performance between two populations. The unit of selection could be individual plants, half-sib families, full-sib families and selfed/inbred ($S_1$ and $S_2$) progenies. Selection based on the visual inspection of individual plant is referred to as phenotypic selection since its genetic worth cannot be known unless the trait under selection has high habitability. On the other hand, selection based on families/progenies is known as genotypic selection, as genetic worth of selected plant is assessed based on its progeny performance. Thus, several intra- and inter-population improvement selection methods are recognized and are described below.

## Intra-population improvement methods

**Mass selection.** Mass selection is the simplest and easiest of all methods and requires the fewest resources and only one generation per cycle. It is effective, particularly if the trait of interest has high heritability. Jan-orn et al. (1976) predicted that mass selection would be effective in improving highly heritable traits like days to flower and plant height in sorghum. It is useful if the population is highly heterogeneous. Mass selection procedures in sorghum have been suggested by Doggett (1968). Mass selection involves selection and recombination of selected plants in a population. A population segregating for male-sterility is planted in isolation. Several superior male-sterile plants are selected based on visual assessment and harvested individually. Equal quantity of seeds from selected plants is bulked to constitute the population for next cycle of selection. Thus, it follows that the unit of selection is individual plant.

Doggett (1972a) has described modified mass selection with alternating male-sterile (female) and male-fertile (male) plants selection in successive generations, aimed at enhancing selection response by increased parental control. In one cycle, seed is harvested from only selected male-sterile plants. These seeds are bulked and sown to constitute the population for the next cycle of selection, wherein, male-fertile plants are selected and harvested seed from selected plants is bulked for selection of male-sterile plants. This procedure is continued. Mass selection should be used in the first few cycles of selection after synthesis of a population. This makes populations reasonably uniform for plant height and maturity before using more sophisticated methods of recurrent selection requiring family/progeny evaluation.

**Half-sib family/progeny selection.** Half-sib selection requires two generations per cycle since it involves progeny testing. Male-sterile plants are tagged at the time of flowering and are allowed for open-pollination. Each head is harvested and threshed separately. A part of the seeds from each head is sown in yield trial (evaluation phase) and the remaining is saved as remnant seed. The best entries are chosen from the yield trials, and the remnant seed from these entries is bulked to constitute the population for the recombination phase. Along with the replicated yield trial of half-sib families as well as other families (which will be described subsequently) for selection of best families to recombine, a separate nursery is planted simultaneously to identify male-sterile plants. Sib-mated male-sterile heads are harvested and bulked with remnant seed of families selected on the basis of grain yield and other selection criteria as appropriate in a yield trial. This bulk is sown to allow random mating in the next season. Again, male-sterile plants are tagged and harvested individually to form the next cycle of evaluation. This method of selection is known as “Half-sib family selection” because the unit of selection is half-sib families and a breeder has control over only one of the parents, ie, male-sterile plants (females). Recombination is carried out in the off-season and evaluation in the main season. The method was used with low selection intensities to improve backup populations (eg, Downs Bulk, Brown Population, WABC, Bulk Y and RS5DX) at ICRISAT and progress was made for overall agronomic desirability, grain quality, and in increasing uniformity for plant height and maturity.

**Full-sib family/progeny selection.** Full-sib families can be developed by crossing selected male-fertile plants onto selected male-sterile plants. The full-sib families so generated are evaluated in a yield trial and the remnant seed of the selected families is then bulked and allowed to recombine. Crosses of male-fertile plants with male-sterile plants are then made and the cycle repeats. In this scheme of selection, the unit of selection is full-sib families and the breeder has the control over both the parents unlike in half-sib family selection.

**$S_1$ family/progeny selection.** It is one of the most effective selection schemes for sorghum (Gardner 1972). $S_1$ family selection requires three generations per cycle. Heads of male-fertile plants are bagged at flowering to ensure selfing, or they can be tagged to ensure that heads from male-fertile plants and not male-sterile plants are harvested at maturity. Selected plants are harvested and threshed separately, each head forming an $S_1$ family. These families are evaluated in yield trials. Remnant seed from the families selected or their sibbed families based on the yield trials is sown, and seed from male-sterile heads are selected to ensure recombination. Seeds from male-sterile heads are then bulked and sown. Male-fertile heads of good plants are identified for testing to begin next cycle. The units of selection and recombination are $S_1$ progenies. The basic concept behind selfed progeny selection is to expose deleterious recessive genes to facilitate their elimination during evaluation and to increase additive genetic variation. Doggett (1972b) reported the first evidence of success of this method and observed, on an average, 25% yield increase per cycle. After one cycle, the improved population produced a higher grain yield than the best varieties. Jan-orn et al. (1976) predicted that $S_1$ family/progeny testing and selection offered the greatest promise for improvement in NP3R, a population developed at the University of Nebraska, whether calculated on a cycle or on an annual basis. $S_1$ testing is very efficient if three generations can be grown a year. This is possible only with very early maturing populations.

**$S_2$ family/progeny selection.** In this scheme of selection process, heads of selected male-fertile plants are bagged at flowering to ensure selfing, or they can be tagged to ensure that heads from male-fertile plants and not male-sterile plants are harvested at maturity. The $S_1$ progenies are grown and plants in $S_1$ progenies rows are selected and again selfed. Selected selfed plants are harvested and threshed separately, each head forming an $S_2$ family. These $S_2$ families are evaluated in yield trials and handled exactly in a manner similar to that in $S_1$ progeny selection and thus selfed/inbred progenies constitute units of selection in both the methods. $S_2$ progeny testing is expected to result in maximum gain per cycle and is most suitable when two growing seasons are available per year, thus permitting one cycle every two years. The method has several advantages over others: additive genetic variance is maximized in $S_2$ families; the families are sufficiently uniform to permit precise evaluation; two generations per year provide sufficient time between the generations for sending seed to test locations in a range of environments and analyzing the data for the selection of lines for recombination; selection for different traits can be done in various generations ranging from half-sib to $S_2$ according to the nature of their inheritance; and the lines evaluated are more homozygous and it is hence easier to extract pure lines. In addition, continuous selfing and evaluation is expected to improve the probability of deriving more vigorous inbred lines. The disadvantage of the scheme lies in the necessity to sib-mate $S_2$ lines to increase the frequency of male-sterile plants for reconstituting the next cycle of the population.

**Testcross family/progeny selection.** This selection method is a slight deviation from the concept of intra-population improvement in the sense that the targeted population is improved based on the evaluation of testcross progenies generated by crossing several selected plants of targeted population with a broad based tester population. Thus, the targeted population is not only improved for *per se* performance but also with respect to general combining ability (*gca*). It essentially involves three steps; (1) self-pollination of male-fertile plants and testcrossing them to a broad based tester, (2) evaluation of testcross progenies in a yield trial and (3) intercrossing of selected plants based on yield trial.

A number of male-fertile plants from the base population are selected and selfed and simultaneously crossed to a broad based tester. The resultant testcross progenies are evaluated in a yield trial to identify promising families, the units of selection. The remnant seed of selected testcross progenies is bulked and sown and allowed for open pollination with male-sterile plants. Seeds from male-sterile heads are then bulked and sown. Male-fertile heads of good plants are identified for testcrossing to begin next cycle. The cyclic nature of selection through testcrosses (with broad based tester) from selfed seed increases the frequency of genes conferring good *gca* and gradually improves the population *per se* performance as well. As the population is improved both for *per se* performance as well as *gca*, the probability of deriving vigorous lines with good *gca* is higher. The choice of the type of tester has been extensively debated. While broad based tester improves *gca,* a narrow genetic-based tester such as an inbred improves specific combining ability (*sca*). The use of low yielding testers, presumably with low frequency of favorable alleles at important loci, have been advocated because they are expected to increase variation in testcross progenies and thus allow better discrimination among the plants to be evaluated in testcrosses (Hallauer and Miranda 1981).

## Inter-population improvement methods

**Half-sib reciprocal recurrent selection.** Comstock et al. (1949) first suggested the use of Reciprocal recurrent selection (RRS), which maximizes the genetic divergence between the two populations for loci with dominance and/or over-dominance effects. The main objective of this method is to develop the two populations simultaneously so that superior inbred lines would be extracted that combine well with each other. In this scheme of selection, each population provides a source material to advance/ improve and also serves as a tester for the other population. Individual selected male-fertile plants (tag or bag these plants for identification at maturity) in one population, designated as 'A' will be crossed to several random male-sterile plants of the other population designated as 'B'. In a similar manner, several selected male-fertile plants of population 'B' are crossed onto several random male-sterile plants of population 'A'. The crosses thus generated are evaluated in a yield trial and seeds from selected male-fertile plants are bulked and grown in isolation. Incorporate heterozygous male-sterile plants into these populations. Allow for random pollination of male-sterile heads. Mark male-sterile plants at flowering. Harvest seed from male-sterile plants in each population and bulk to constitute the new populations from which male-fertile plants would be selected and crossed to male-sterile plants from the other population and the cycle repeats. This method is useful in sorghum since hybrids are commercially viable and large inter-population heterosis is observed. There are two types of RRS depending on the identity of the parents involved in the crosses; (1) half-sib RRS and (2) full-sib RRS. Half-sib RRS is the most promising in sorghum because it provides a better evaluation of males to be selected. In half-sib RRS method, random male-fertile plants (their identity is not maintained) of one population are crossed onto male-sterile plants of the other population to generate half-sib families for evaluation in yield trial and thus half-sib families form units of selection. The subsequent steps are as described above.

**Full-sib RRS.** In this method, only selected male-fertile plants of one population (their identity is maintained) are crossed onto several selected male-sterile plants of the other population to generate full-sib families for evaluation in yield trial and thus full-sib families become units of selection. Since identity of both female and male plants is known, this method is called full-sib RRS. The use of RRS in sorghum, especially full-sib RRS, is hampered by the sterility system used to enable random mating. All crosses (test and selection units) would be generated using the male-sterile as the female for which no selfed seed can be produced. Thus, from the selected full-sibs, only the male parents from each cross can be used as recombination units, effectively reducing selection intensity and failing to capture genes from those female parents producing superior crosses.

Reciprocal full-sib selection has been used to improve the sorghum populations $KP9BC_0$ and GTPP7R, a derivative of TP24. Nearly 200 reciprocal full-sibs from each population (with the other population as male parent) were tested collaboratively by Kansas State University (KSU) at Garden City and the University of Nuevo Leon in Monterrey, Mexico. The top 15% full-sibs were selected from the best stress site, and remnant $S_1$ seed of the male parents of the selected full-sibs was used for recombination. Estimates of genetic variances, heritabilities, and intra-population predicted gains were reported by Chisi (1993). Estimates for the genetic variability and mean were found to be consistently higher in the TP24×KP9B (TP24 as female) than the KP9B×TP24 reciprocal crosses, suggesting that significant cytoplasmic effects may exist (Rattunde et al. 1997).

## Population improvement programs at ICRISAT

Population improvement programs were followed extensively at ICRISAT during the initial periods of its inception. However, during later periods, it received less emphasis due to changes in funding patterns, donors' emphasis on short-term impact and the requirement of national programs. Population improvement programs at ICRISAT, Patancheru, Andhra Pradesh, India were initiated in 1973 with the introduction of a large number of populations (ICRISAT 1974) from Kansas State, Nebraska and Purdue Universities (USA), Serere (Uganda), Nigeria and from Australia using genetic male-sterility induced by $ms_3$ and $ms_7$ genes following recurrent selection procedures to breed for wider adaptability. New backup and advanced populations were synthesized by intercrossing selected progenies from populations of similar maturity, geographic origin, and restoration behavior (Bhola Nath 1977). Backup populations were selected under low selection intensity to maintain variability for a long time. However, the backup populations were later discontinued to reduce the size of the program. The advanced populations were subjected to rigorous selection, with the objective of producing superior varieties and hybrid parents. Initially when resources were abundant, half-sib/$s_1$/$s_2$ family selection methods were followed to improve the populations. However, due to subsequent diminishing resources, simple mass selection alternated with recombination methods became corner stones of developing trait-specific broad genetic-based populations (Reddy et al. 2004). Over the years, an array of 19 populations (Fig. 25) for long-term improvement for key agronomic traits or trait combinations and resistance to major insect pests and diseases were developed using $ms_3$ and $ms_7$ genes and improved at ICRISAT, Patancheru (Reddy et al. 2005).

The populations developed by ICRISAT and NARS collaborators in the Southern African region target contrasting agro-ecological zones (ICRISAT 1989, Rattunde et al. 1997). *Guinea* and *caudatum* and *guinea*×*caudatum* populations have been developed in Mali (Rattunde et al. 1997). In Southern Africa, the four random mating populations developed jointly by ICRISAT and national agricultural research systems (NARS) using $ms_7$ gene provided broad genetic-based gene pools from which national programs and South African Development Committee (SADC) could develop improved lines and varieties using recurrent selection (Obilana 1989).

## Utilization of populations

The economic benefits of population improvement are ultimately realized when readily usable genetic variability for traits of interest from these populations is effectively exploited to develop pure-lines and/or hybrid parents. It is towards this goal that populations are improved by recurrent selection. It is assumed that as the mean performance of a population is improved, there will be a parallel improvement in the performance of its derived progenies (Eberhart 1972). The probability of deriving pure-lines with desired combination of genes is higher from an improved population with higher frequency of desirable alleles. Studies at ICRISAT have given good indications that it will work. A set of random $S_1$ progenies from different cycles of two populations were evaluated for grain yield in two trials (Prasit 1981). The contribution of the most advanced cycles in each population is the highest, followed by the previous cycle, indicating that as the average grain yield of populations increased, the grain yield of the derived lines also increased.


*Fig. 25. A high-tillering forage population developed at ICRISAT, Patancheru.*

Traditional pedigree selection methods used during the inbreeding produce pure-lines for direct use as varieties or hybrid parental lines or, more frequently, as improved parental lines for use in pedigree breeding activities. Purging of GMS gene/s from the derived lines is essential if it/they has/have been used for building the populations. Selection against the male-sterile gene can be easily handled by identifying sterile plants at flowering. The lines from the populations are produced by successive selfing of male-fertile plants at any stage until the progeny becomes uniform. Continued selection for male-fertile plants eliminates male sterility from the lines. This approach has been used in the development of lines from $S_1$ families originating in several populations at Purdue (Rattunde et al. 1997), and in the ongoing derivation of restorer lines and dual-purpose varieties out of the US/R (DP) population at ICRISAT.

At ICRISAT, the process of identifying superior lines began in the early stages of population development. For example, a line from the Diallel population has been released as Melkamash in Ethiopia (Table 9). A foliar resistant line A 2267-2 is derived from US/R population at ICRISAT and is extensively used as one of the parents in sorghum breeding programs in China, Ethiopia and Latin America. Several hundred pairs of cytoplasmic-nuclear male-sterility-based seed parents (A-) and their corresponding maintainer lines (B-) have been developed in an array of maturity and plant types. The male sterile line SPL 132A (renamed as 421A by China) developed from Diallel population at ICRISAT is directly used as female parent in development and release of five hybrids, Liao Za 4, 6, 7 and 10 and Jin Ja 94, in China (Table 9).

**Table 9: Examples of successful utilization of populations at ICRISAT.**

| Variety | Population | Place of release | Released name | Year of release |
|---|---|---|---|---|
| Diallel Pop-7-682 | Diallel | Ethiopia | Melkamash | 1982 |
| A 3681 | FLR | China | Yuan 1-98 | 1982 |
| A 3872 | Bulk Y | China | Yuan 1-28 | 1982 |
| A 3895 | Bulk Y | China | Yuan 1-505 | 1982 |
| A 6072 | Indian Synthetic | China | Yuan 1-54 | 1982 |
| SPL 132A (renamed as 421A in China) | Diallel | China | Liao Za -4, -6, -7 and -10 and Jin Ja 94 | 1988 |
| M 36248 | WABC | Myanmar | YEZIN 2 (Schwephyu 2) | 1984 |

Source: Reddy et al. 2004.

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