*ISBN: 978-81-968830-0-3*

# 9. Breeding Methods for Cross-Pollinated Crops

**Dr. S. K. Kaushik**

Senior Scientist (Genetics & Plant Breeding),
RVSKVV, KVK-Ujjain, MP.

***Abstract***

*Breeding methods for cross-pollinated crops aim to enhance desirable traits through controlled mating. Techniques such as recurrent selection, hybridization, and population improvement are utilized to improve yield, quality, and resistance to biotic and abiotic stresses. Recurrent selection involves cycles of mating and selection to gradually improve populations. Hybridization creates superior hybrids by crossing genetically diverse parents. Population improvement selects and improves diverse populations for specific traits. These methods facilitate the development of cultivars with increased productivity and adaptability, contributing to sustainable agriculture and food security. Efficient application of these techniques relies on a comprehensive understanding of genetics and breeding principles.*

***Keywords:***

*Food Security, Selection, Diversity, Hybridization, Adaptability, Sustainability*

## 9.1 Introduction:

The roots of agriculture extend deep into human history, marking the transition from nomadic lifestyles to settled communities. With the cultivation of crops came the recognition of the need for improvement — a quest to enhance traits such as yield, adaptability, and resistance to environmental challenges. Cross-pollinated crops, with their reliance on external agents for pollination, presented both opportunities and challenges in this endeavor. Plants served the best to human being through supplying the source of food.

They directly supply 90 per cent of human calorie intake and 80 per cent of the protein intake. However, approximately 30,000 plant species occurring on the earth, nearly 40 crop species provide the majority of calorie and protein to human beings with 50 per cent being contributed by nine species of cereals. They may face the danger of extinction and thereby create an ecological imbalance. Moreover, they may also suffer from poor yield and quality, let alone their assured supply. In order to overcome these fear and deficiencies, useful plant ought to be domesticated and brought under cultivation. Once the concept of crop cultivation is developed, minimizing its cost together with maintaining the quality of usable plant products becomes imperative. The intricate world of plant breeding unfolds against the backdrop of a dynamic and evolving agricultural landscape. As we embark on the exploration of breeding methods in cross-pollinated crops, it is essential to establish the fundamental principles that govern this field. The preface serves as a gateway to our journey, providing context, significance, and a glimpse into the complexities that define the breeding strategies employed in crops reliant on cross-pollination. Plant breeding is the art and science of changing the genetics of plants for the benefits of humankind. Plant breeding can be accomplished through many different techniques ranging from simply selecting plants with desirable characteristics for propagation, to more complex molecular techniques. Plant breeding has been practiced for thousands of years, since near the beginning of human civilization. It is now practiced worldwide by individuals such as gardeners and farmers, or by professional plant breeders employed by organizations such as government institutions, universities, crop-specific industry associations or research centers.

International development agencies believe that breeding new crops is important for ensuring food security by developing new varieties that are higher-yielding, resistant to pests and diseases, drought-resistant or regionally adapted to different environments and growing conditions. Crop improvement refers to the genetic modifications of plants to satisfy human needs. Through a long history of trial and error, a relatively few plant species have become the mainstay of agriculture and thus the world's food supply. This process of domestication involved the identification of certain useful wild species followed with a process of selection that brought about changes in appearance, quality, and productivity. The selection process was unconscious in many cases e.g. for "non-shattering" types in wheat. For some crops a directional or clear conscious selection occurred, especially when the variant was obvious and would be maintained by vegetative propagation e.g. seedless banana.

The changes in domestication included alteration in organ size and shape; loss of many survival characters, such as bitter or toxic substances; disarticulation of seeds in grains; protective structures, such as spines and thorns; seed dormancy; and changes in life span—increased in crops grown for roots or tubers and decreased in crops grown for seed or fruit. Mass selection is a powerful tool/technique for making rapid changes easily while maintaining genetic diversity in the population. The selection of naturally occurring variants is the basis of crop improvement. Over thousands of years this technique resulted in the development of modern basic crops. As humans carried improved crops to new locations, opportunities opened to increase genetic variation from natural intercrosses with new wild populations.

In the eighteenth and nineteenth centuries a conscious attempt was made to predict the performance of plants that could be expected over seed generations. Furthermore, it became obvious that variation could be managed by controlling the mating process, Thepedigree selection, was found to increase the efficiency of the process. Progeny testing (evaluating the genetic worth by progeny performance) increased efficiency of this process. The origins of commercial plant breeding began in the second half of the nineteenth century among seed producers. It involved controlled crosses (hybridization) between selections to control genetic recombination, followed by selection of improved types. This is still the basis of traditional plant breeding. Interestingly much of this early type of plant breeding was carried out without a clear understanding of the genetic mechanism involved in inheritance.

Until the famous experiments of Gregor J. Mendel (1822–1884) with the garden pea the basic theory of inheritance involved the concept of blending. Mendel unraveled the basic concept of inheritance and clearly showed that characters in the pea were due to elements, later called genes, that remained unaltered as they were inherited. Many characters in peas, such as tallness and dwarfness, were shown to be controlled by a pair of genes, of which one member was not always expressed (the concept of dominance and recessiveness). Mendel demonstrated that the gametes of the pea contained one member of the gene pairs that controlled characters and that recombined randomly at fertilization. Mendel's paper was published in 1866, but it had no impact until the paper was "rediscovered" in 1900, when it created a sensation. It was soon obvious that the differences in appearance among plants (phenotypes) could be explained by the interaction of various genes (genotypes) as well as interaction with the environment.

## 9.2 Twentieth-Century Developments:

In the twentieth century plant breeding developed a scientific basis, and crop improvement was understood to be brought about by achieving favorable accumulations and combinations of genes. Taking advantage of known genetic diversity could facilitate this, and appropriate combinations were achieved through recombination brought about by the sexual process (hybridization). Furthermore, it was possible to move useful genes by special breeding strategies. Thus, a gene discovered in a wild plant could be transferred to a suitable adapted type by a technique known as the backcross method. A sexual hybrid was made, followed by a series of backcrosses to the desirable (recurrent) parent, while selecting for the new gene in each generation. After about five or six back-crosses, the offspring resembled the recurrent parent but contained the selected gene.

In the early twentieth century it was demonstrated that the extra vigor long associated with wide crosses (called hybrid vigor or heterosis), particularly in naturally cross-pollinated crops, could be exploited in plant breeding. For maize, a new system of hybrid breeding was developed, using a combination of inbreeding and outbreeding. Inbreeding was accomplished by crossing the plant with itself. This led to a decline in vigor as the step was repeated over several generations. Outbreeding was achieved by intercrossing the inbred lines to restore vigor. The hybrid between inbreds derived from divergent inbreds (called a single cross or $F_1$ hybrid) was uniform (homogeneous), and some were superior to the original populations before inbreeding. During the process of inbreeding, the inbreds became weak, but vigor was restored in the $F_1$. To increase seed set from weak inbreds, two hybrids were crossed; this was known as the double cross method. Hybrid maize breeding led to enormous increases in productivity, which were soon exploited in a wide variety of seed-propagated crops, including naturally self-pollinated ones, such as tomato and rice. A number of genetic techniques were developed and refined in twentieth-century breeding, such as improved techniques to search for and store increased genetic variability, different techniques to develop variable populations for selection, and improved methods of testing to separate genetic from environmental effects. The exact details of the process for crops necessarily differed among naturally cross-pollinated plants (such as maize) and naturally self-pollinated plants (such as soybean or tomato) as well as those plants in which vegetative propagation (usually cross-pollinated) permitted the fixing of improved types directly.

Conventional plant breeding can be defined as systems for selection of superior genotypes from genetically variable populations derived from sexual recombination. The system is powerful because it is evolutionary; progress can be cumulative, with improved individuals continually serving as parents for subsequent cycles of breeding. Genetic improvement by conventional breeding has made substantial changes when the efforts have been long-term. Characters improved include productivity, quality, and resistance to diseases, insects, and stress. There are, however, limits to the progress of conventional breeding. These are due to limitations of the sexual system, because it is usually not possible to incorporate genes from nonrelated species or to incorporate small changes without disturbing the particular combination of genes that make a particular type unique. Thus, a useful gene in cabbage cannot be transferred to wheat. Limitations of conventional breeding are particularly apparent when a needed character (such as disease or insect resistance) is unavailable in populations that can be incorporated by sexual crosses. Mutations may be induced, but they are often deleterious or connected with undesirable effects.

Suitable manipulation of cultivation practices and parameters can reduce the cost of crop-cultivation and increase the production per unit area. But there is always a limit to such manipulations warranted by the nature of crop, type of genotype, prevailing agro-ecological conditions, etc. for example, if a crop is cross-pollinated, even the best crop husbandry cannot create a homogeneous crop and thereby uniform products. If suitable varieties are not available for problem area like drought prone, or alkaline/ saline soil and so on, very little is possible to realize a reasonable yield. Similarly, if the very genetic potential of the plant is poor, no agronomy can enhance the yield-levels beyond a certain limit i.e. old and tall varieties of wheat and rice having low yield potential due to frequent lodging and poor response to inputs. Besides, crop management is basically related to the manipulation of external factors (soil, water, inputs etc) having nothing to do with the heritable or genetic constitution of crop plants. Now, the role of plant breeding comes in, offering to alter the genetic potential of crop plants for the better. It renders a desirable permanent (heritable) change in the nature of the plant and thus elevates its genetic ceiling for productivity and quality, as well as transforms it into a more stable cultivar adaptable over a wide range of edaphoclimatic conditions. However, the fact that plant breeding changes the genetic background of crop plants is not so straight. The simple reason is that crop plants vary greatly with respect to their modes of reproduction and pollination- the two basic features associated with perpetuation of generation. Plants are categorized into following three categories based on reproductive systems:

- Sexually or seed propagated plants (SPP)
- Asexually or vegetatively propagated plants (VPP)
- Combined or vegetatively + seed propagated plants (VSPP)

Further, the SPP and VSPP may differs distinctly in the mode of pollination, thus can be grouped as:

a. Self-pollinated/inbreeders/autogamous plants.
b. Cross-pollinated/outbreeders/allogamous plants.
c. Often cross-pollinated plants with 5-10 per cent cross pollination and 90-95 per cent self-pollination.

These modes of pollination or mating systems in plants are naturally linked with their floral structure, flowering behavior, and gametogenesis, etc. in fact, the flower provides the base for pollination and hence the locale for artificial genetic manipulation of the resulting progeny(seeds). Since plant breeding entails desirable alterations in the genetic composition of progenies, an adequate understanding of the two basic features of generational continuity (i.e. reproduction and pollination) is the essential ingredient of the genetic improvement programme. These features are appropriately elaborated together with floral biology, gametogenesis, mechanisms of pollination control, etc. In addition to the above factors associated with the nature of crop with which plant breeding concerns, the latter is also practically interlinked with other factors related to crop management, crop growth and development, its interaction with pests and pathogens, its biochemical parameters, and so on. This is precisely because these aspects are of immense significance in realizing the genetic potential fixed by plant breeding for elevated crop production. As such, plant breeding is viably connected with other disciplines of science dealing with corresponding aspects, like agronomy, plant physiology, entomology, plant pathology, biochemistry, etc. the biotechnological approach (cellular breeding, i.e. tissue culture, and molecular genetics, i.e. genetic engineering) is an advance frontier-the current phase of plant breeding. Thus, the science of plant breeding, coupled with a working knowledge of these associated disciplines related to plant (crop) performance, aims for a rapid stride in crop improvement to feed the evergrowing world population.

## 9.3 Scope of Crop Improvement:

A higher yield is strictly demanded due to stagnate or decreasing area under crop cultivation. This goal is depended upon the genetic improvement of crop plants through appropriate breeding methods which are the key to augment the food supply for increasing world population. There are majorly two ways by which yield improvement is possible:

### I. Enhancing the productivity of crops:

increase in crop yield per unit of area, time and input can be achieved:

a. Through proper management of soil and crops involving suitable agronomy and harnessing physical resources.
b. Through high potential crop varieties created by appropriate genetic manipulation of crop plants.

### II. Stabilizing the productivity achieved:

External factors like diseases and pests coupled with unfavourable natural vagaries, tend to minimize the gain realized in crop productivity. The stabilization of productivity can be accomplished:

a. By using suitable fungicides/ pesticides to protect the crop from diseases/ pests invading the crops.
b. By growing disease/pest resistant crop varietiesevolved through genetic manoeuvring.
c. By using crop varieties that are bred specially for wide adaptation or for specific crop zones to offset the ill-effects of unfavourable environmental conditions prevailing in the area.

Although suitable agronomy and chemical measures adopted for disease control can increase and stabilize crop production to a great extent, they involve substantial cost and are to be repeated everytime.

In contrast, creation through breeding of high potential disease free crop varieties is, by and large, much costly and confers stable and permanent advantage to the farming communities. Allard (1966) writes "in one way, the contribution to human welfare made by superior varieties is the most satisfying of all methods of increasing production. Normally such varieties add nothing to the cost of production beyond that required to handle the additional increment of yield. The appeal of this situation to human nature is undeniable."

It would certainly not be out of place here to record the possible advancement made in crop production through plant breeding researches carried out for the development of high yielding varieties in crop plants. It would show how efficiently the food famine in some countries could be averted, and on the other hand, it would raise an immense hope to excel our past performances.

Indian agriculture remained stagnant particularly during the early sixties. Long spells of severe drought during 1965 and 1966, and a serious outbreak of diseases in some parts of the country led some futurologists of affluent countries to profess a possible doom in India by the end of the decade. However, as a result of the gradual replacement of the inefficient crop varieties by the efficient ones with respect to productivity (production per unit of are, time and input), and supported by infrastructural facilities, we achieved a breakthrough in quite a few cereal crops, such as rice, wheat, pearmillet sorghums and maize.

The average yield of wheat, which was about 7 q/ha duting 1947, had gone up to 14 q/ha in 1976.in Punjab, the average yield rose to 23.6 q/ha in 1974-75. During the same period the Pearlmillet production crossed the targeted limit of the Fouth five-year Plan (recorded 8 million tons of grain yield compared with 7 million tons of target fixed). Similar gains were achieved in sorghum and maize also. This became possible through the exploitation of the improved strains of wheat and of hybrids and composite populations in pearl millet, sorghum and maize. The serious disease problem of downy mildew in pearl millet was successfully resolved and new resistant hybrids were developed. Thus, the prophets of doom were proved wrong. An area of "green revolution" was ushered in, and India was able to tide over its food problem efficiently. An examination of table1 reveals the fast pace of food grain production vis-à-vis the population growth in India from 1966 to 1974.

Away from home, it has been estimated that the annual production of corn in the USA has been increased by 750 m. bu by growing hybrid corn alone. In western Europe, the yields of wheat and barley have been accelerated by nearly 1 per cent per annum since the late 1940s. perhaps the most dramatic impact of plant breeding accrued in Mexico.

In the 1950s, it had an average yield of wheat of about 8 q/ha which by 1966, more than trebled as ar result of the stimulus from CIMMYT-a Rockfeller Foundation programme on crop improvement. Consequently, a wheat importing country was changed in to wheat exporting country due to surplus wheat production during the 1960s.

Thus, plant breeding has made a tremendous contribution in increasing the crop yield in diminishing its susceptibility to natural hazards that limits its productivity. These achievements, by far no less than voyages to space, have opened new vistas and possibilities of further improvement in cultivated crops. However, there are many constraints which tend to limit the advancement sought in crop improvement.

## 9.4 Factors limiting Genetic Improvement of Crop Plants:

The breakthrough achieved in a few cereal crops need not instantly warrant a similar success in other cereal and non-cereal crops. Many obstacle that a breeder generally confronts with in his breeding programmes, tend to restrict the pace of progress under crop improvement. Factors of major consequences are distinguished as under:

**A. Narrow genetic base:** The presence of genetic variability in the breeding material is the pre-requisite, particularly at the initial stage, for a breeding programme to succeed. Almost all the cultivars are developed by exploitaing this variation, "though each variety is evolved in its unique fashion". Variability is, however, depleted rapidly due to genetic drift and genetic erosion in limited or finite material. Therefore, lack of variability, if not promptly replenished, would fail to record success commensurate with the efforts and resources involved.Perhaps the most important is the use of a limited number of genes and kinds of cytoplasm for crop improvement. For instance, *Norin* dwarfing gene and *timopheevi* cytoplasm in male sterility of wheat, opaque-2 and T-cytoplasm of maize, *Dee-Gee-Woo-Gen* gene in rice, and Milo and Tifton sources of male sterility in sorghum and Pearlmillet, respectively are widely used by respective crop breeders. This obviously confers an inherent hazard of genetic uniformity of the crops, thus rendering them vulnerable to possible epidemics, such as leaf-blight epidemic that occurred in the American maize carrying T-cytoplasm in 1970.

**B. Absence of suitable plant type:** The concept of a model ideotype envisage a plant which commands the physiological efficiency to exploit most usefully all the available resources including soil nutrients, agronomic management and solar energy so as to realize the maximum theoretical yield. Such a capacity is usually conferred to the plant by the exploitation of developmental traits.

**C. Unpredictable genotype-environment interaction**: The efficiency of breeding procedures in terms of speed of advance is greatly influenced by the presence of g x e interaction. Inadequate choice of environment for exercising selection in segregating generations may lead to genetic slippage due to buffering effect of environmental agencies during selection process. It also determines the adaptive specificities of crop varieties and thus plays a significant role in crop adaptation over time and space.

**D. Small population size and indiscriminate experimental design**: The small size of $F_2$ population and the low number of $F_3$ families grown and retained, and the lack of sensitive design fail to eliminate the effects of plant competition and soil heterogeneity. They also fail to permit detection of small genetic differences between selections, particularly during the early segregating generations, thus causing slow or little progress in plant improvement.

Moreover, unscientific deployment of genetical principles tends to aggravate the situation further.

**E. Inherent genetic barriers**: Serious genetic bottlenecks inherent in the crop material itself sometimes restricts its rapid improvement by ordinary breeding methods. Major genetic bottlenecks generally encountered by plant breeders are:

**F. Negative Genetic Association:** Correlations between desirable and undesirable traits, i.e. high protein and low grain yield in most of the cereals, long fibre and low lint yield in cotton, etc. are not conducive for rapid improvement.

a. **Limited fixable component and Low Heritability:** This arises mostly in highly domesticated material where, consequent upon selection, additive genetic variance is rapidly exhausted. Such a situation results in the plateauing of progress with no further response to selection.
b. **Correlated response:** Negative genetic association particularly due to pleiotropy or developmental correlations adversely affect the selection for a desirable trait.
c. **Maternal Effects:** Occuring either due to additive maternal effects or due to maternal interaction, it masks the genetic variances and thus renders the breeding procedures less effective. However, it may be useful also particularly in seed parent(females) involved in hybrids. For instance, in $F_1$ hybrids. The females' lines in such hybrids may give better hybrid vigour, if they carry maternal effects particularly due to maternal interaction.
d. **Linkage Disequilibrium:** Occuring mainly due to extreme proximity of genes on the chromosomes, it sets in a deadlock in the population which loses its dynamic structure and becomes static. Then it shows little or no response to improvement by selection.
e. **Genetic Asymmetry:** Arising due to directional dominance and directional gene frequency in the population, it causes a lack of response to selection, hence, a slow pace of the progress.
f. **Non-realization of hybrid vigour**: Sometimes heterosis fails to occur due to mutual cancellation of the components of heterosis. This leaves a breeder many a time perplexed in his hybrid programme.
g. **Inability to Exploit Hybrid Vigour**: In many selfers like wheat and barley where substantial hybrid vigour has been observed but their breeding systems (Self-pollination) and non-availability of suitable seed parent (e.g. male sterile lines) impose restriction on the exploitation of hybrid vigour.

There are many more shortcomings and difficulties that are likely to be faced during the process of crop improvement. In brief, as Allard and Hansche (1964) pointed out, the reason for slow progress is either inadequate variability at the initial stage or the lack of systematic sampling of the total range of variability or small population size and high selection pressure or non-understanding of the procedures employed for the exploitation of the existing variability.

Subsequently, Krull and Borlaug (1970) also stated that slow progress in varietal improvement has been due to the lack of imagination, vision and efficiency in incorporating the existing variability into improved varieties, rather than the lack of available variability.

In fact, standard breeding methods are inadequate to explore the range of useful variability for complex characters, because they are incapable of growing and testing large number of progenies, and of providing repeated intermating required for recombination. However, in view of the significant advancement made hitherto by the active participation of man in natural evolutionary processes, there is every reason to believe that difficulties will be surmounted and progress streamlined.

## 9.5 Population Improvement:

Populations of cross-pollinated crops are highly heterozygous as well as heterogenous. The genetic constitution of allogamous crops show variable inbreeding depression. Consequentlythe goal of breeding methods for these crops is preventing inbreeding, or atleast to keep it to the minimum in order to avoid its undesirable effects. The breeding methods commonly used for outbreeders may be grouped into two major categories:

(i) population improvement and (ii) hybrid and synthetic varieties. In case of population improvement, mass selection or its modifications are used to increase the frequency of desirable alleles, thus improving the characteristics of populations.

Population improvement was old-age method employed to cross-pollinated crops. Mass selection has been used by farmers since early days which played a significant role in the improvement of outbreeders. The interest in population improvement methods declined with the development of hybrids and synthetic varieties. However, breeders are now paying increasingly more attention to population improvement programmes since the last decades. The maize improvement programme at CIMMYT, Mexico and the Pearlmillet improvement programme at ICRISAT, Hyderabad, are largely based on population improvement.

## Breeding Methods of Improvement:

The population improvement’s breeding methods may be grouped into the following categories: (A) Methods without progeny testing and (B) methods with progeny testing. A more comprehensive and commonly used classification of selection schemes is presented in table 2.

- **A. Breeding methods without progeny testing**: In this group, plants are selected on the basis of their phenotype, and no progeny test is carried out e.g. mass selection.
- **B. Breeding methods with progeny testing**: The breeding methods in which plants are initially selected on the basis of their phenotype, but the final selectionof plants that contribute to the next generation is based on a progeny test. This class of population improvement methods includes progeny selection or ear-to-row method, and recurrent selection.

## 9.6 Aims of Selection:

In selfers, selection is employed to isolate plants with superior genotypes. These plants are then used to establish separate purelines or their seeds are bulked to produce a mixture of purelines.

This is possible because selfers are naturally homozygous and generally donot show appreciable inbreeding depression.

On other hand, outbreeders generally show moderate to severe inbreeding depression. Consequently, (1) inbreeding must be avoided or kept to a minimum in outbreeders. Further, (2) individual plants from such crops are highly heterozygous. The progeny from such plant would be heterogeneous and usually different from the parent plant due to segregation and recombination. Therefore, desirable genes can be seldom fixed through selection in cross-pollinated populations, except for qualitative traits and, perhaps, for easily observable quantitative characters with high heritability. (3) The breeder, therefore, aims at increasing the frequency of desirable alleles in the populations. (4) This is expected to lead to an increase in the frequency of desirable gene combinations of genotypes. As a result, the phenotype of the population would be favourably changed in the direction of the selection.

Hence, the genotype of the individual plants of cross-pollinated species is generally of little importance, particularly in population improvement programmes. It is the frequency of desirable genes or alleles in the population as a whole that determines the value of a population.

### 9.6.1 Mass Selection:

In Mass selection, a number of plants are selected based on their phenotype, and the open-pollinated seed from them is bulked together to raise the next generation. The selected plants are allowed to open-pollinate, *i.e.*to mate at random, including some degree of selfing. Hence, in this method no control on pollen parent because selection of plants is based on the maternal parent only without progeny testing. Mass selection, as applied to cross-pollinated crops is essentially the same as that applied to self-pollinated crops; a generalized scheme for the method is outlined in Figure 9.1.

The selection cycle may be repeated one or more times to increase the frequency of favourable alleles; in such a case, the selection scheme is generally known as phenotypic recurrent selection. Care should be taken to select a sufficiently large number of plants in order to keep inbreeding to a minimum level. The efficiency of mass selection primarily depends upon the number of genes controlling the character, gene frequencies and, more importantly, heritability of the concerned trait.

### A. Advantage of Mass Selection:

- It is the simplest breeding programme. The work of Breeder is minimum in this method since selection is based on the phenotype of plants.
- The selection cycle is very short, *i.e.* only one generation. Thus, in every generation, one cycle of selection is completed.
- It is highly efficient in improving easily identifying characters that have high heritability, e.g. plant height, size of ear, date of maturity, etc.
- If proper care is taken, mass selection is effective in improving yield of cross-pollinated crops. Most cross-pollinated crops have a high additive component of genetic variance, which responds to selection.

- Since the improved strains are likely to be similar to the original population in the range of adaptation, extensive yield trials may not be required before its release as a new variety.

### B. Disadvantage of Mass Selection:

- Selection of plants is based on the phenotype of individual plants. Most of the quantitative characters are considerably affected by the environment. Therefore, superior phenotype is often a poor basis for the identification of superior genotype.
- The selected plants are pollinated by both superior and inferior plants present in the population because selected plants are allowed to open-pollinate. This reduces the effectiveness of selection.
- High intensities of selection reduce population size and, as a result, lead to some inbreeding. Inbreeding depression may nullify the advances made under selection.

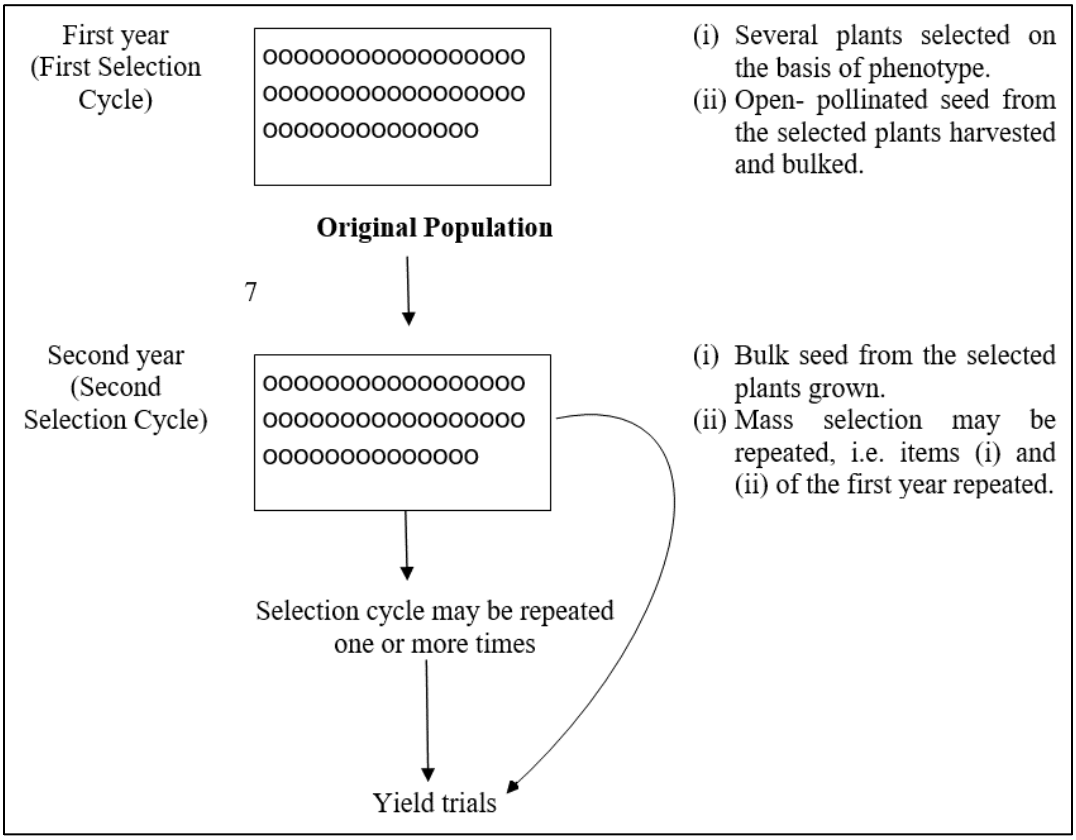


**Figure 9.1: Mass selection as applied to cross-pollinated crop species. When the selection is repeated one or more times, as outlined above, the scheme is known as phenotypic recurrent selection**

## 9.6.2 Modifications of Mass Selection:

There are two basic lacuna of mass selection, *viz.*,

(i) lack of control of the pollen source and (ii) the confusing effect of the environment on the of individual plant's expression, can be corrected by suitable modifications of the selection scheme; these modifications are briefly described as follows:

A. Superior plants in the field are allowed to open-pollinate whereas remaining inferior plants are detasselled. This modification exercises some control on the pollen source but the identification of inferior plants should be based on only those characters, which are expressed before flowering.

**Table 9.1: A summarized description of the various selection schemes for population improvement.**

| Selection scheme | Brief description |
|---|---|
| **Intrapopulation Improvement** | For improvement within a population. |
| A. Mass Selection | Selection based on the phenotype of individual plants; selected plants reproduce by open pollination. |
| 1. For one sex | All plants in the population allowed to produce pollen; open pollination without any restriction. |
| 2. For both sexes | Inferior plants present in the population are detasselled; open-pollination among the remaining plants. |
| 3. Stratified | Field divided into small plots of about 40 plants each; selection within small plots; open pollination without any restriction; selection usually for one sex. |
| 4. Contiguous control | Plants of a constant genotype (single cross, inbred) used as check and planted after every 2-4 hills for comparision; check plants detasselled; others open-pollinate; selection usually for one sex. |
| B. Family Selection | Selection based on means of individual plant progenies or families. |
| 1. Half-sib | Plants within each family (individual plant progeny) are half-sibs, i.e., have one parent (usually the female) in common. |
| a. Ear-to-row | Families produced by open-pollination; selection within superior families; no replicated trial; unrestricted open-pollination among all the families. |
| b. Modified ear-to-row | As in ear-to-row; superior progenies identified by replicated yield trial; pollen source; a random bulk of all the families. |
| c. Half-sib selection | As in the ear-to-row, but only superior progenies planted in the crossing block and allowed to open-pollinate. |

| Selection scheme | Brief description |
|---|---|
| d. Modified half-sib | Half-sibs used for yield trial; S1 families from plants producing superior half-sibs intermated through open-pollination. |
| e. Broad base testcross | Half-sib families produced by crossing the selected plants to a tester with a broad genetic base (parental or unrelated) used for yield trial; $S_1$ progenies from plants producing superior half-sib families intermated (syn.,recurrent selection for GCA). |
| f. Narrow base testcross | As in the broad base testcross, but the tester has a narrow genetic base (syn., recurrent selection for SCA). |
| 2. Full-sib | Plants within each family are full-sibs; produced by mating the selected plants in pairs. |
| a. Full-sibs intermated | Full-sibs used for yield trial; superior full-sibs intermated. |
| b. $S_1$ progenies intermated | Full-sibs used for yield trial; $S_1$ progenies from plants producing superior full-sibs intermated |
| 3. Inbred or selfed | Families produced by selfing. |
| a. $S_1$ | Families produced by one generation of selfing used for evaluation; superior families intermated (Syn., simple recurrent selection). |
| b. $S_2$ | Families obtained by two generations of selfing used for evaluation; superior families intermated. |
| **Interpopulation Improvement** | Two populations improved simultaneously for combining ability with each other. |
| A. Half-sib reciprocal recurrent selection (HS-RRS) | See the description for reciprocal recurrent selectiongiven in the text. Two modifications suggested by Paterniani (the second modification requires at least two ears/plant). |
| B. Full-sib reciprocal recurrent selection (FS-RRS) | Each selected plant in the populations A and B is selfed. Each selected plant from A is testcrossed with one selected plant from B. the testcrossed progenies are evaluated in field trial. $S_1$families of plant from A producing superior testcross progenies are intermated; the same is done for those from B. requires atleast two ears/plant in one of the two populations. |

B. Pollen from all the selected plants is collected and bulked and then used to pollinate the selected plants. This scheme ensures full control on the pollensource, but it can be applied to only those characters, which can be selected for before pollen shedding.

C. **Stratified Mass Selection**: This modification is also known as the **grid method of mass selection** which issuggested by Gardner in 1961. The selection field is divided into several small plots, *e.g.* having 40-50 plants each. Equal number of superior plants are selected from each of the small plots, *i.e.* selection is done within the plots and not among the plots. The seed from all the selected plants is composited to raise the next generation. The basis for this modification is the consideration that variation due to environment, including heterogeneity in soil fertility, will be much smaller within the small plots than that in the whole field. Thus, selection within the plots is expected to be more effective than that without any stratification. Stratified mass selection has been able to increase the yielding ability of an open-pollinated variety of maize. Hays Golden, by about 3% per cycle (or generation) for 15 generations. Response to selection for improved yield has continued in Hays Golden even after 30 cycles of selection.

D. Plants of a constant genotype, *e.g.* a single cross hybrid, are planted as checks after every one, two or four plants of the variety under selection. The yields of plants under selection are expressed as per cent of the yield of the nearest check plant. This scheme is designed to minimize the environmental influence on the yields of plants being selected. It employs the principle of contiguous control.

### 9.6.3 Effectiveness of Mass Selection:

Hallauer and Miranda (1981) summarized the results from selection studies using mass selection. Mass selection has effectively improved characters with high heritability in maize, *e.g.* ear height, lodging resistance, ear type, adaptiveness, oil and protein contents, resistance to *Helminthosporium* leaf bight, days to flowering (tasselling as well as silking), prolificacy and stalk volume, and in other crop species.

Stratified Mass selection found effective in selections for increased as well as decreased yields, and for changed ear length, kernel size and maturity in maize. The results from 26 studies on mass selection for higher yields are summarized in table 20.2.

The yield increased at an average rate of 3.5% per cycle of selection; the increases ranged from -1.0 to 19.1 per cent/cycle, the most common estimates being 1.1 to 3.4% per cycle. The gains under selection for other quantitative characters, *e.g.* prolificacy and ear height, appear to be relatively more than those for yield possibly due to a lower heritability for the latter. Selection for prolificacy, *i.e.* increased number of ears per plant, as well as that for single eared plants is highly effective in changing the yields of the selected populations. It is not surprising since prolificacy has high positive correlation with grain yield in maize.

Mass selection is an effective selection method for most traits, but often correlated responses for other traits are in the undesirable direction. Therefore, proper controls must be used during selection.

For example, in one study, increased prolificacy in maize was the primary trait of selection, but maturity, plant health, root and stalk strength and grain moisture were also considered in choosing plants in each selection cycle. This resulted in favourable correlated responses for grain yield, grain moisture and performance index, while days to mid-silk, plant height and root and stalk lodging remained stable over the cycles of selection.

**Table 9.2: Effectiveness of mass selection in changing yield and yield traits in maize.**

| Criterion of selection | Number of reports | Selection cycles | Change in the character under selection/cycle (%) | | |
|---|---|---|---|---|---|
| | | | Mean | Range | Most common estimates |
| Yield | | | | | |
| Increased | 26 | 2-15 | 3.5 | -1.0-19.1 | 1.1-3.4 |
| Decreased | 2 | 1 | 8.2 | 0.7,15.7 | |
| Prolificacy | | | | | |
| Increased | 11 | 1-11 | 4.7 | 2.0-11.4 | 2.0-4.4 |
| Decreased | 2 | 1,11 | 4.5 | 1.5, 7.5 | |
| Ear Height | | | | | |
| Increased | 2 | 5,6 | 5.2cm | 2.5, 7.9cm | 2.0-3.2cm |
| Decreased | 6 | 4-12 | 3.5cm | 2.0-7.9cm | |
| Ear Length | | | | | |
| Increased | 1 | 10 | 1.6 | | |
| Decreased | 1 | 10 | 3.2 | | |
| 100-Seed Weight | | | | | |
| Increased | 1 | 9 | 2.0 | | |
| Decreased | 1 | 9 | 2.0 | | |

## 9.7 Selection Schemes with Progeny Test:

### 9.7.1 Progeny Selection:

The simplest form of progeny selection is the **ear-to-row method,** which has been extensively used in maize. The method was developed by Hopkins in 1908. In its simplest form, the ear-to-row method of selection is as follows (Figure 9.2, Scheme I).

a. A number of plants are selected based on their superior phenotype. They are allowed to be open-pollinate, and the seeds from individual plants are harvested separately.
b. A single row of 10-50 plants *i.e.,* a progeny row, is grown from each selected plant. The progeny rows are evaluated for desirable characters and superior progenies are identified.
c. Several phenotypically superior plants are selected from the superior progenies. There is no control on pollination, hence, the plants are permitted to open-pollinate.
d. Small progeny rows of 10-50 plants (as in item 2), are grown from the selected plants, and the process of selection is repeated.

It should be seen that this scheme is relatively simple and that the selection cycle is of one year only.

However, it suffers from the defect that plants in the superior progenies are pollinated by those in both the superior and inferior progenies; this reduces the effectiveness of selection.

**Modification of Ear-to-Row Method:** In order to overcome the defect described above, the following modifications may be used (Figure 9.2, Scheme II).

**First Year.** Several Plants are selected on the basis of phenotype (as in item 1 above). Allow the selected plants to open-pollinate and harvested separately.

**Second Year**. Small progeny rows are grown (as in item 2 above) and evaluated. The remaining seed from each of the selected plants is kept separately. Superior progenies are identified.

**Third Year.** The remaining seeds from plants which showed superior progenies (identified in the second year) is bulked and planted in the third year. This constitutes the selected version of the population. Plants are allowed to open-pollinate.

A number of plants are selected on the basis of phenotype and the selection cycle may be repeated one or more times.

This modification of ear-to-row method was widely used in breeding of maize and was responsible only are allowed to mate among themselves. But for each selection cycle, two years are required as compared to only one in the case of ear-to-row method.

**Modifications of Progeny Selection**: Several modifications of the ear-to-row method of selection are available and many more may be devised to suit the specific needs of the breeder. Some of the modifications are briefly described below.

a. Seed for progeny testing are obtained by selfing the selected plants only. This variation is the basis for ***simple recurrent selection,*** and is also known as ***$S_1$ family selection.*** When the seeds for progeny test are obtained after two generations of selfing, the scheme is known as ***$S_2$ family selection.***

***b.*** The seeds for progeny testing are obtained by crossing the selected plants to a common tester. The common tester may be an open-pollinated variety, a hybrid or an inbred. This variation has been refined as ***recurrent selections for general and specific combining abilities*** andreciprocal ***recurrent selection.***

***c.*** The progeny test having a replicated yield trial inspite of a single row. In this method, the real value of each progeny can be estimated more precisely by separating the environmental effects. This modification was proposed by Lonnquist in 1964, and is by far the most successful method of progeny selection. The progenies from the superior plants are planted in a replicated yield trial and in a crossing block (recombination or seed production plot). The progenies in the crossing block are detasselled. These progenies are pollinated by the pollen from the rows of a random bulk of all the selected progenies planted after every 2-3 progeny rows. Superior progenies are identified on the basis of the yield trial. Best plants from the superior progenies in the crossing block are selected and their seeds are harvested separately. The progenies from the selected plants are handled in the same way as outlined above. In this scheme (1) the evaluation of progenies is based on a replicated trial, (2) the source of pollen is controlled, and (3) each selection cycle is completed in one year. This scheme is commonly known as ***modified ear-to-row method.***

***d.*** Seeds for progeny test are obtained by mating the selected plants in pairs so that the plants within a progeny are full-sibs, *i.e.,* have both the parents in common. This is commonly known as ***full-sib family selection.***

**Advantages of Progeny Selection:** The schemes of progeny selection, except recurrent selection, have the following advantages.

a. The selection of individual plants is based on progeny test rather than phenotypes which give more accurate reflection of the genotype than phenotype. Thus, progeny selection is far more efficient than mass selection in the identification of superior genotypes.
b. Inbreeding depression may be avoided by selecting a large number of not closely related plant progenies.
c. The selection scheme is still relatively simple and easy. But some of the modifications are more complicated and tedious.

**Disadvantages of Progeny Selection**: The progeny selection schemes, other than recurrent selection, suffer from the following defects.

a. In most progeny selection scheme plants are allowed to open-pollination. Hence, there is no control on pollination and the selection is based on the maternal parent only. This reduces the efficiency of selection.

b. Many of the progeny selection scheme are complicated and involve considerable work.

c. The selection cycle is usually of two years, *i.e.* the complete selection process takes two years. Thus, the time requirement for selection is doubled than of mass selection.

## 9.7.2 Applications of Mass and Progeny Selections:

Mass selection has been extensively used for the improvement of cross-pollinated crops. In case of maize, heterosis breeding almost completely replaces mass selection but mass selection is a renewed interest in population improvement. Heterosis breeding demanding time and labours becoming expensive, complicated and requires strict pollination control. Resultantly in most of allogamous crops heterosis breeding is not likely to become economically feasible. Hence, mass selection or one of the other population improvement schemes is likely to remain the common breeding method. Mass selection has been used to maintain varietal purity of allogamous crops whereas in some crops, progeny selection is used for the same purpose. These population improvement schemes have been used and are being used for the development of new improved varieties of many allogamous crops.

## SCHEME I

| | | | |
|---|---|---|---|
| **FIRST YEAR** | 0000000<br>0000000<br>0000000<br>0000000<br>Original population | i. Plants selected on the basis of phenotype.<br>ii. Open-pollinated seed from each plant harvested separately | First selection cycle |
| **Second Year** | \|\|\| \|\|\|\| \|\|\|\| | (i) Small progeny rows grown from the selected plants.<br>(ii) Superior progenies are identified.<br>(iii) Phenotypically superior plants selected from the superior progenies<br>(iv) Plants allowed to open-pollinated & seed harvested separately. | Second Selection cycle |
| **Third Year** | \|\|\|\|\|\|\| \|\|\| | As in items (i) to (iv) in the second year | Third selection Year |
| | May Be repeated one or more times<br>**Yield Trials** | | |

## SCHEME II

| | | | |
|---|---|---|---|
| FIRST YEAR | 0000000<br>0000000<br>0000000<br>0000000 | (i) Same as in items (i) and (ii) of the first year in Scheme I. | First selection cycle |
| Second Year | \|\|\|\|\|\|\| \|\|\|\|<br>*Plants producingsuperior* | (i) And (ii) as in second year of scheme I.<br>(ii) The remaining seeds from the plants (selected in the first year) producing superior progenies bulked to raise the next generation. | |
| Third YEAR | 0000000<br>0000000<br>0000000<br>0000000 | (i) The bulk seed [year 2, item (iii) planted.<br>(ii) Plants allowed to open-pollinate.<br>(iii) Plants with superior phenotype selected and seed harvested separately | Second Selection Cycle |
| **Fourth Year** | \|\|\|\|\|\|\| \|\|\|<br>May be repeated one or more times<br>**Yield Trials** | As in items (i) to (iv) in the second year | |

**Figure 9.2**: **Depicted the Ear-to-row method of progeny selection (Maize).**

## 9.8 Recurrent Selection:

Hayes and Garber (1919) firstly suggested the idea of recurrent selection and independently by East and Jones in 1920. However, cohesive breeding schemes of recurrent selection were developed after 1945 when Hull suggested that specific combining ability may be improved by recurrent selection.

The recurrent selection schemes were devised in relation to heterosis breeding. The idea was to ensure the isolation of superior inbreds from the populations subjected to recurrent selection for their ultimate utilization in the production of hybrid and synthetic varieties.

The probability of isolation of a superior inbred line depends primarily on two factors;

(1) the proportion of superior genotypes present in the base population from which inbreds are isolated, and (2) the effectiveness of selection during the inbreeding process in increasing the frequency of desirable genes or gene combinations. The available evidence clearly indicates that selection is ineffective in preventing a random fixation of genes even with mild inbreeding. Thus, even with strict selection, one cannot hope to enhance, to an appreciable extent, the chances of isolating an outstanding inbred line from a population. Therefore, the only course open to the breeder is to increase the frequency of favorable genes and genotypes in the base population, using a breeding scheme that would keep inbreeding to a minimum.

The recurrent selection scheme are variations of progeny selection, the difference lying (1) In the manner of obtaining the progeny for evaluation, and (2) in making the all-possible intercrosses among the selected lines in place of open-pollination. There are following four different types of recurrent selection schemes, each being suited for a specific purpose:

(1) simple recurrent selection, (2) recurrent selection for general combining ability (RSGCA), (3) recurrent selection for specific combining ability (RSSCA), and (4) reciprocal recurrent selection (RRS).

### 9.8.1 Simple Recurrent Selection:

In this**,** (1) a number of plants having desirable phenotype are selected and self-pollinated. (2) In the second year. Separate progeny rows are grown from selfed seeds of each selected plants. (3) The progenies are intercrossed in all possible combinations by hand, and equal number of seeds from each cross is composited to produce the next generation.

This completes the ***original selection cycle.*** For recurrent selection, several desirable plants are selected from the composited population obtained from the original selection cycle; they are selected on the basis of phenotype and are self-pollinated.

Next year, progeny rows are grown from the selfed seed and all possible intercrosses are made by hand. Equal seeds from all the intercrosses are composited to produce the next generation. This constitutes the **first recurrent selection cycle**. The population may be subjected to one or more recurrent selection cycles (Figure 9.3).

In case the character or characters under selection can be easily and accurately measured on individual plants, which are selected and selfed, the above scheme is followed as such. But some other characters can be measured from seed only, *e.g.,* oil and protein contents.

In such cases, the selfed seeds from the selected plants are evaluated for the characters under selection. Selfed seed from the plants that are superior for the concerned character(s) are used for planting separate progeny rows. The rest of the above scheme is followed as such without modification. It may be seen that the scheme (Figure 9.3) is very similar to the scheme I of progeny selection (Figure 9.2) However, it differs from the scheme I as follows:

(1) the selected plants are self-pollinated as compared to open-pollination in scheme I, (2) the progenies are intercrossed in all possible combination and not open-pollinated as in Scheme I. and (3) individual plants are selected from the reconstituted population (in the third year) and not from the individual plant progenies (in the second year) as is done in scheme I. The scheme may be modified to include progeny test for characters with low heritability e.g., yield. A portion of the self-pollinated seed from the selected plants is used to plant

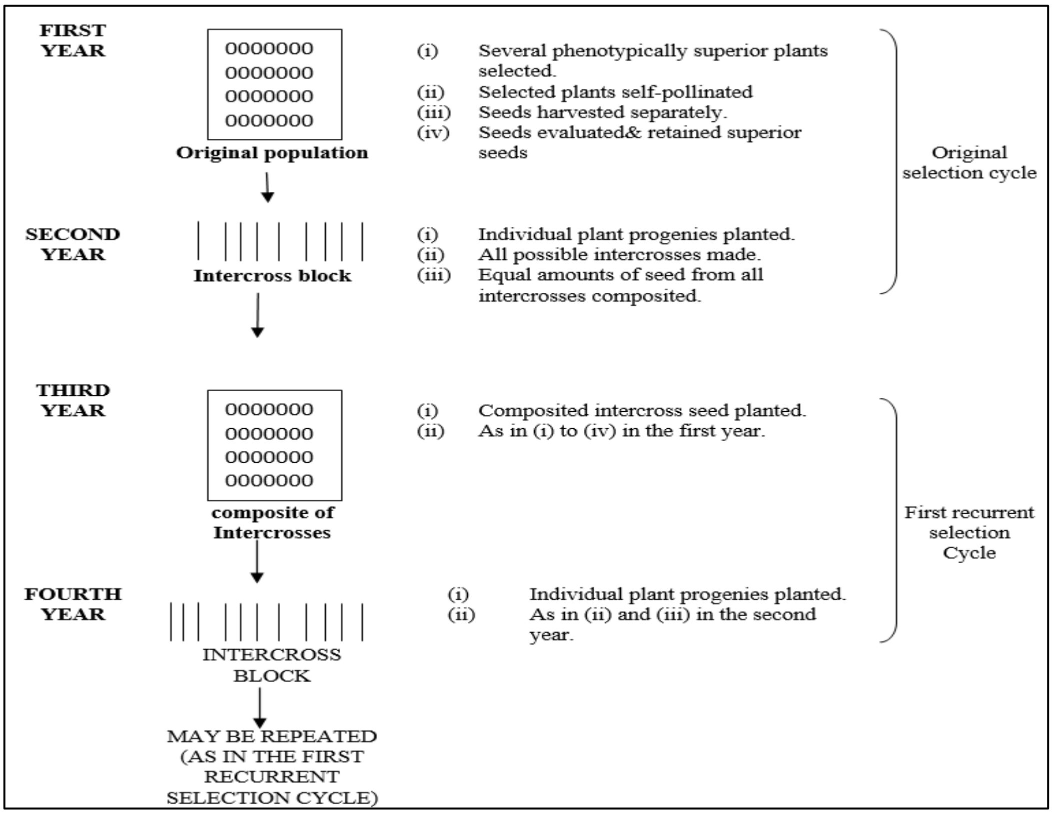


**Figure 9.3: Simple recurrent selection when the characters under selection can be easily evaluated on the basis of phenotype of the selected plants or form the selfed seed obtained from them.**

progeny rows, preferably replicated, which are evaluated for the character under selection and superior progenies are identified. Next year the remaining selfed seed from the plants producing superior progenies is planted in progeny rows for intercrossing. All possible intercrosses are made by hand. Equal seed from each intercross is mixed together to raise the next generation. This modification is very similar to the Scheme II of progeny selection (Figure 9.2). The differences between these two are the same as mentioned above. Recurrent selection is effective in increasing the frequency of desirable genes in the selected population. It is the most suited for characters with high heritability. The mean of selected population shifts in the direction of selection. Generally, there is no appreciable reduction in variability, and in some cases selected populations may show a relatively larger variation than the original population. Simple recurrent selection is considerably more efficient than selection with self-pollination. There is a relatively low inbreeding, and if care is taken it can be kept to a minimum. Inbreeding can be minimizedas: (1) the population derived from the mixture of intercrosses may be allowed to mate at random for one generation, and this open-pollinated seed should be used to establish the population for reelection. Alternatively, (2) each intercross may be grown separately and it should be ensured that the selected plants are not related by parentage or by descent, *i.e.*, the plants are not selected from a few of the intercross only.

## A. Recurrent Selection for General Combining Ability (RSGCA):

In this case, a tester strain having broad genetic base is the common parent mated to a number of selected lines, strains or plants. A set of crosses(progenies) is made and such a set of progenies used for the estimation of general combining ability of the lines or plants. A tester with a broad genetic base implies a population that has a large genetic variation, *e.g.*, a multiple cross. Since the gametes from such tester would be variable, the differences between plant x tester progenies would be primarily due to the general combining ability (GCA) of the plants because the tester being common to all such progenies. It is, therefore, assumed that the plants selected on the basis of superior performance of their plant x tester progenies would have superior GCA. Jenkins (1935) suggested that RSGCA is a direct outgrowth of early testing. Early testing is the testing of inbreds for combining ability in the early stages of inbreeding *e.g.*, in the first or second selfed generation. In 1940 Jenkins proposed a scheme (essentially RSGCA) for developing synthetic varieties from short-term inbreds. The various steps involved in RSGCA are schematically represented in Figure. 4, and are briefly outlined below.

- **First Year:** A number of phenotypically superior plants are selected from the source population (an open-pollinated variety or a synthetic or an advanced generation of a hybrid). Each selected plants is selfed and harvested separately and seeds saved for planting in the third year. Each selected plants also crossed (as male) to a number of randomly selected plants from a tester with broad genetic base. The test-cross progeny (plant x tester progeny) from each selected plant is harvested separately and used for a replicated yield trial in the second year.
- **Second year**: A replicated yield trial is conducted using the plant x tester progenies. The superior progenies are identified.
- **Third Year**: The selfed seeds (from the first year) from those plants that produced superior test-cross progenies (indentified on the basis of yield trial in the second year)

are planted in separate progeny rows in a crossing black. These progenies are intercrossed in all possible combinations. Equal amounts of seeds from all the intercrosses are composited to obtain the next generation. This completes the original cycle of selection.

- **Fourth Year:** The seeds obtained from bulking of all the intercrosses is planted as the source population for the first cycle of recurrent selection. Based on phenotype several plants are selected. Each of them is selfed as well as crossed (as male) to number of random plants from the tester with wide genetic base.
- **Fifth year:** The activities as second Year are repeated.
- **Sixth year:** Operations of the third year are repeated. Now it is completed the first recurrent selection cycle.
- **Seventh Year:** The second recurrent selection cycle may be initiated as in the case of the first recurrent selection cycle in the fourth year. In this manner several cycles of recurrent selection may be carried out.

The RSGCA is effective in changing GCA in the direction of selection. In addition, RSGCA is also effective in increasing the yielding ability of population. At the end of recurrent selection cycle, the population is made up of equal amounts of seeds from all possible intercrosses among a number of progenies selected on the basis of their general combining ability (Figure 20.4). Obviously, this population is identical with a synthetic variety. The yielding ability of such a variety developed through recurrent selection may be further improved through additional cycles of selection. Generally, owing to inbreeding, variability may be decrease in the selected population. This could be prevented adopting simple recurrent selection. RSGCA can be used for two basically different purposes. (1) It may be used to improve the yielding ability and the agronomic characteristics of a population. In this case the end product of selection is used as a synthetic variety. (2) Alternatively, it may be used to accumulate genes for superior GCA. The end product of selection is then used for the isolation of inbreds with superior GCA. It is expected that the frequency of such inbreds would increase after a few cycles of RSGCA.

## B. Recurrent Selection for Specific Combining Ability (RSSCA):

Firstly, it was proposed by Hull in 1945. The isolation of lines from a population that will combine well with a given inbreds is the objective of RSSCA. It is assumed that a large part of heterosis is the result of non-additive gene action, i.e., dominance and epistasis. This part of heterosis will, therefore, depend on specific gene combinations and is designated as specific combining ability (SCA). If plants are selected on the basis of performance of their progeny derived from testcross with an inbreds, they would be selected for their combining ability with the inbred used as tester. It may be expected that these plants would have genes or gene combinations that specifically combine well with the genes present in the tester inbred. The procedure for RSSCA is identical with that for RSGCA, except that in RSSCA an inbred is used as a tester in the place of an open-pollinated variety. The tester must be an outstanding inbred because it would be one of the parents of the hybrid that would be produced using the inbred lines isolated from the improved population. Therefore, great care must be exercised in the selection of the inbred (tester) in an RSSCA programme. The RSSCA selection scheme is briefly outlined below (Figure. 4) while referring to the Figure. 9.4 the tester should be read as an outstanding inbred.

i. **First Year.** Several plants are selected from the population and self-pollinated. The selected plants (used as males) are also crossed to an outstanding inbred used as the tester (used as female).
ii. **Second Year.** A replicated yield trial is planted using the testcross progeny. Outstanding progenies are identified.
iii. **Third Year.** Selfed seeds from the plants that produced the outstanding progenies are planted in separate progeny-rows in a crossing block. All possible intercrosses among these progenies are made by hand. Equal number of seeds from all the intercrosses are composited; this completes the **original selection cycle.**
iv. **Fourth year.** The composited intercross seed is planted and the operations of the first year are repeated.
v. **Fifth Year.** Operations of the second year are repeated.
vi. **Sixth Year.** Operations of the third year are repeated. This completes the first recurrent selection cycle. The population may be subjected to one or more recurrent selection cycles. If desired, by repeating the operations of the first recurrent selection cycle (fourth to sixth years).

## C. Reciprocal Recurrent Selection (RRS):

Comstock, Robinson and Harvery (1949) proposed this selection scheme. The objective of RRS is to improve two different populations in their ability to combine well with each other. In this scheme, each of the two populations, say A and B, serve as tester for the plants selected from the other population. For example, a random sample of plants from population A serves as the tester for the plants selected from population B. Similarly, a random sample of plants from population B serves as the tester for those selected from population A. It may be seen that this selection method effects selection for both GCA and SCA. It selects for GCA because the two testers (populations A and B) have broad genetic base since they are genetically heterogenous. Selection for SCA is accomplished because the two populations (or inbreds derived from them) would be crossed with each other to produce the commercial variety, and the plants in each of the source populations are selected for their ability to combine well with the gene combinations present in the other populations, *i.e.* for SCA with each other, A generalized scheme for RRS is outlined below (Figure 9.5).

A. **First year:** Several plants are selected from the population A and B on the basis of their desirable phenotype. Each of the selected plants from population A is crossed as male with several randomly selected plants from the population B used as female. Similarly, each of the plants selected from the population B is crossed as male with a random sample of plants from the population A used as female. All the selected plants are allowed to selfing and the selfed seed is harvested separately and is stored for use in the third year. All the testcross seeds from an individual selected plant are composited and later used for progeny test in the second year (Figure 9.5).
B. **Second Year:** Two replicated yield trials are conducted. One trial is for the testcross progenies of the plants selected from population A, while the other one is for those of the plant selected from population B. On the basis of these progeny tests, plants (of both population A as well as B) producing superior testcross progenies are identified.
C. **Third Year:** Selfed seed from the plants selected on the basis of progeny tests (in the second year) are planted in two separate crossing blocks as individual plant-progeny

rows. In one crossing block, seeds from the plants selected from population A are planted, while in the other crossing block seeds from plants selected from population B are sown. Within each crossing block, all possible intercrosses among the plant progenies are made. Equal number of seeds from all the intercrosses in the crossing block A are mixed to raise the next generation of population A. Similarly, the next generation of population B is raised from the seed obtained by mixing equal amounts of seed from all the possible intercrosses in the crossing block B. This completes the **original selection cycle.**

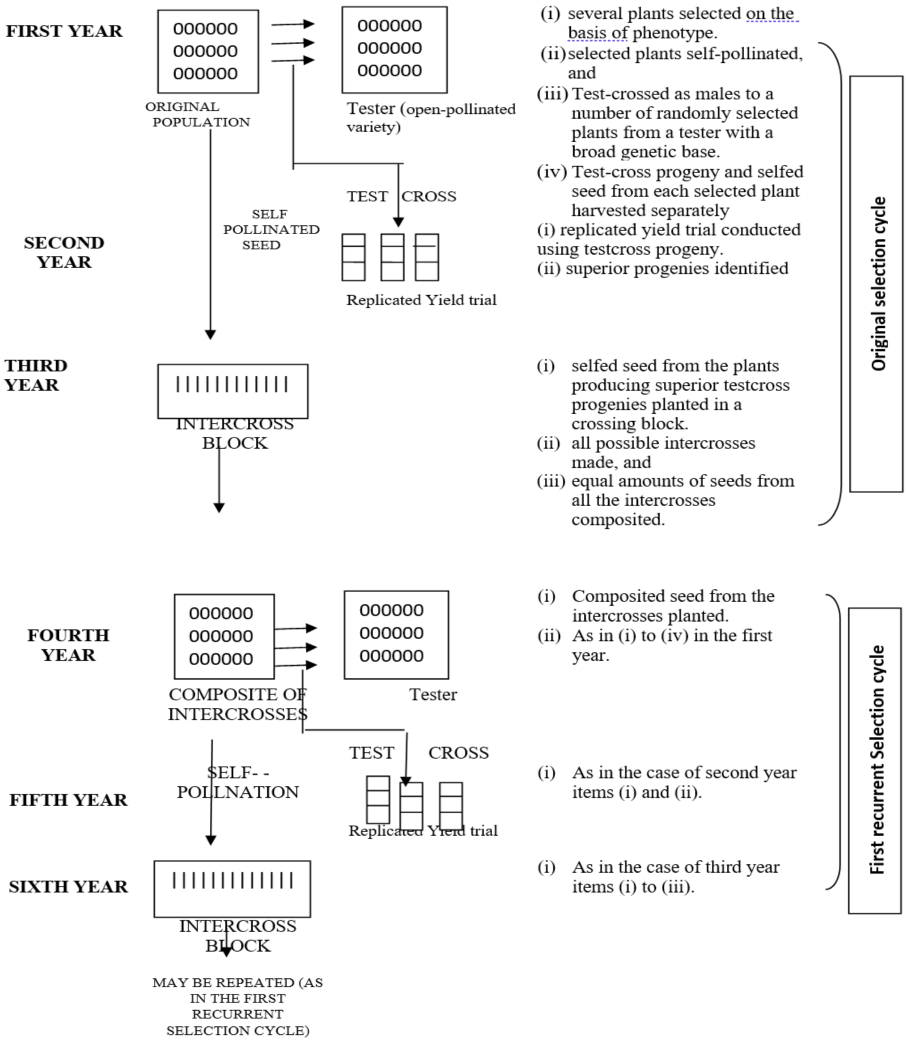


**Figure 9.4: Scheme of Recurrent selection for general combining ability (RSGCA). In RSSCA, an inbred is used as a tester in the place of an open-pollinated variety; the rest of the scheme remains same.**

**D. Fourth Year.** Populations A and B are planted from the composited seed from all the intercrosses in blocks A and B. respectively. Operations of the first year are repeated.

**E. Fifth Year.** Operations of the second year are repeated.

**F. Sixth Year.** Operations of the third year are repeated.

This completes the first **recurrent selection cycle**. The population may be subjected to further selection cycles, if desired, by repeating the operations of the first recurrent selection cycle. The two populations developed by RRS may be used in one of the following two ways:

**a. Production of A Synthetic Variety**. The two populations may be intermated to produce a superior population with a broad genetic base. This is similar to a varietal cross, but in this case the populations have been subjected to selection for combining ability (both GCA and SCA) with each other. In maize (Z. mays), crosses between populations improved by reciprocal recurrent selection show higher yields than those between the original populations.

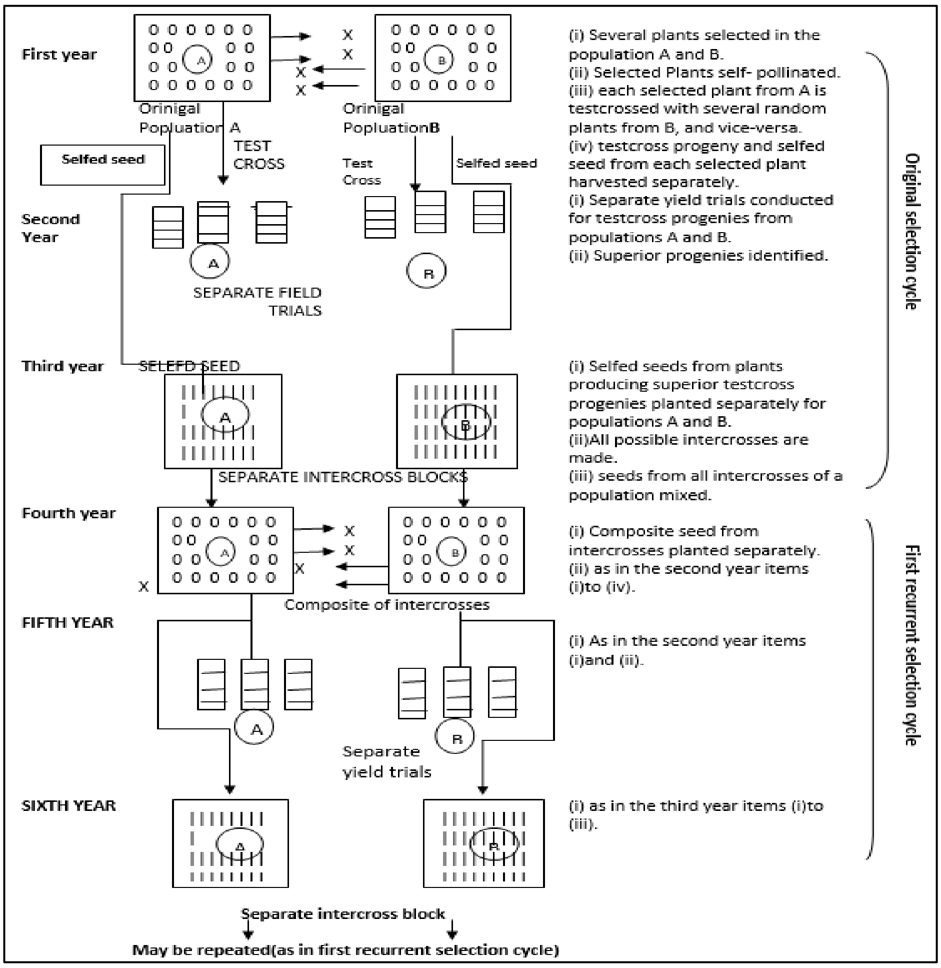


**Figure 9.5: Reciprocal recurrent selection. Two populations, A & B, with broad genetic base serve as testers for each other.**

**b. Isolation of Inbred Lines.** Inbreds may be isolated from the improved versions of populations A and B. These inbreds may then be crossed to produce a double cross or a single cross. In this case, the inbreds should be crossed in the following order.

- Single cross: ($A_1$ x $B_1$)
- Double cross: ($A_1$ x $A_2$) X ($B_1$ x $B_2$)

Where, $A_1$ and $A_2$ are two inbreds isolated from the population A, and $B_1$ and $B_2$ are the inbreds isolated from population B. This would permit the maximum expression of heterosis in the double cross. There is considerable evidence that reciprocal recurrent selection increases the yielding ability of hybrid produced by crossing inbreds isolated from the selected populations.

## 9.9 Comparative effectiveness among Different Recurrent Selection Schemes

On theoretical grounds, the following relationships may be expected among the three recurrent selection schemes, viz., RSGCA, RSSCA and RRS.

A. In case of incomplete dominance, the effectiveness of Reciprocal Recurrent Selection (RRS) and Recurrent Selection for GCA would be comparable and superior over Recurrent Selection for SCA.
B. In case of complete dominance, the effectiveness of all the three schemes *i.e.* Reciprocal Recurrent Selection (RRS), Recurrent Selection for GCA and Recurrent Selection for SCA would be equal.
C. In case of over dominance, RRS and RSSCA would be equally effective, but both would be more effective than RSGCA.
D. The above relationships are true when there is no epistasis, and there is absence of multiple alleles and linkage disequilibrium. Genetic studies with most crop species clearly demonstrate that these assumptions are unrealistic. In most situations, epistasis is important and linkage disequilibrium and multiple alleles are likely to be present. In such cases, RRS would be superior to RSGCA and RSSCA.
   Thus theoretically, in almost all practical situations, RRS may be expected to be superior to RSGCA and RSSCA.

## 9.10 Effectiveness of Progeny Selection Schemes:

There is considerable literature on the effects of various progeny selection schemes on yield and yield traits in crops. Hallauer and Miranda (1981) described the information regarding maize and is summarized in table 20.3.

Ear-to-row effectively improved highly heritable traits e.g., oil and protein contents, but failed to improve yielding ability due to the reason other than deficiency of the selection scheme. The reason for this one is (1) poor field plot technique during selection and evaluation, (2) contamination from foreign pollen, and (3) inbreeding depression due to small experimental populations. This failure was fruitfully results in the development of hybrid varieties. The modified ear-to-row scheme proposed by Lonnquist in 1964 is highly effective in improving the yield of maize (average gain 4.8 % per cycle).

**Table 9.3: Effectiveness of the various progeny selection schemes in improving the yield of maize populations.**

| Selection Scheme | Number of reports | Number of selection cycle | | Increase in yield/ cycle (%) of the population per se | | Increase in yield/cycle (%) of the testcrosses | |
|---|---|---|---|---|---|---|---|
| | | **Mean** | **Range** | **Mean** | **Range** | **Mean** | **Range** |
| **Ear-to-row** | 4 | 8.5 | 7-10 | 0.5 | -0.2-0.9 | | |
| **Modified ear-to-row** | 6 | 5.8 | 3-12 | 4.8 | 1.8-13.6 | | |
| **Broad base testcross*<br><br>(RS for GCA)** | 19 | 2.1 | 1-4 | 10.2 | -0.5-22.0 | 5.8 | 1.5-14.7 |
| **Narrow base testcross<br><br>(RS for SCA)** | 17 | 2.8 | 2-5 | 5.2 | -2.0-10.3 | 4.9 | 1.0.14.7 |
| **Full-sib family selection** | 12 | 4.2 | 1-10 | 5.3 | 2.5-10.6 | | |
| **$S_1$ family selection (simple recurrent selection)** | 6 | 3.3 | | 4.6 | 1.1-6.9 | | |
| **$S_2$family selection** | 2 | 5.0 | | 2.0 | 1.9-2.2 | | |
| **Half-sib reciprocal** | | | | | | | |
| **recurrent selection** | 13 | 3.8 | 2-8 | | | | |
| **Population A** | | | | 3.9 | -0.1-10.0 | 5.3 | 0.8-17.0** |
| **Population B** | | | | 3.6 | -1.1-15.0 | | |
| **Full-sib reciprocal** | | | | | | | |
| **Population A** | 1 | 3 | | 6.0 | | 3.2** | |
| **Population B** | | | | 5.7 | | | |

* Comparisons were made with either the original variety or a commercial hybrid,e.g., US13.

** Testcross is the cross between the two populations A and B.

Full-sib-family selection is extremely effective in improving yields (5.3% per cycle). Although, inbred ($S_1$ and $S_2$) family selections are also effective in improving yields, but the per cent of change per cycle is comparatively lower than modified ear-to-row and full-sib- family selection (Table 9.3).

Selfed progeny ($S_1$ and $S_2$) selection is more effective and popular method over mass selection for selection of traits other than yield particularly for increased pest resistance. Selfed progeny selection has effectively improved resistance of maize to European corn borer (first and/or second brood) and stalk rot (Table 9.4).

$S_1$ progeny selection improved pest resistance, but correlated effects on grain yields were not desirable. In all the cases, 2 or 3 cycle of recurrent progeny selection were effective. It has been suggested that selfed progeny selection should be limited to 2-3 cycle, and after that either full-sib or half-sib selection should be resorted to. However, the reasons for apparent ineffectiveness of long-term selfed progeny selection are not clear (Hallauer, 1991).

Recurrent Selections for GCA and SCA effectively improved the yields of populations themselves (average gain 10.2 and 5.2% per cycle, respectively). These schemes also improved the GCA (measured as the yield of testcrosses) of the populations the rate of change being slightly higher for RSGCA than that for RSSSCA.

Reciprocal recurrent selections (RRS) improved the yielding ability of the populations themselves as well as that of the population crosses. Use of full-sibs in RRS appears to be relatively more effective than the use of half-sibs in improving the yielding ability of the two populations, but in improving the yields of the populations crosses the latter appears to be more effective.

Comstock and coworkers initiated reciprocal recurrent selection (haif-sib) in 1949 in the population Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic No. 1 (BSCB). Initially, selection emphasized grain yield. But subsequently, other agronomic traits were also included in selection indices, and effective population size was kept between 10 and 20.

The yields of the two populations (BSSS and BSCB) increased by-2% per cycle (indirect response), while that of the population cross increased by 6.6% per cycle (direct response). The estimate of average heterosis increased from 25.4% in cycle zero to 76% in cycle 11 (Table 9.5). Increase in grain yield was not associated with detrimental effects on stalk quality or maturity; in fact, it was associated with markedly reduced stalk lodging. Direct response (increase in the yields of population crosses) was consistent up to cycle 9. But there was a suggestion that a plateau had been reached during the cycles 9 to 11 (table 20.5).

It was concluded that the increase in grain yield with selection resulted from change in allectic frequency of genes with additive and dominance effects in the population BSSS and with primarily dominant effects in BSCB. The indirect responses (increases in the yields of the two selected populations) were comparable in magnitude to the direct response if adjustments were made for the effects of genetic drift.

**Table 9.4: Effectiveness of selfed progeny selection for disease and insect pest resistance in maize (Based on Hallauer, 1991).**

| Pest/pathogen/disease | Base Population | Progeny selection | Change in | |
|---|---|---|---|---|
| | | | **Resistance** | **Yield** |
| **European corn borer (Ostrinianubilails), first generation** | Five synthetic Cultivars | $S_1$ (3 cycles) | Acceptable levels of resistance | - |
| | | | | |
| **Stalk rot (Diplodiazeae)** | Lancaster Sure Crop | $S_1$ (3 cycles) | Significant Improvement | None |
| | | | | |
| | | $S_1$ (7 cycles) | Rating-0.26* per cycle | -1.2q/ha per cycle |
| **European corn borer** | Synthetic cultivar | $S_1$ (4 cycles) | >25% reduction in infestation rating** | >17% reduction |
| **first and second** | BS9 | | | |
| **broods** | | | | |

* Stalk rot of rating of base population, 3.27; that of selected (7$^{th}$ cycle) population, 1.33.

** Infestation rating for first generation of European corn borer: base population, 3.6; selected population (4 th cycle), 2.7; for second generation: base population, 6.4; selected population (4$^{th}$ cycle),4.4.

**Table 9.5: Effects of 11 cycles of haif-sib reciprocal recurrent selection for yield in maize (based on Hallauer, 1991).**

| Selection cycle | | Grain yield (q/ha) | |
|---|---|---|---|
| | BSSS | BSSS x BSCB (Population cross) | BSCB |
| **0** | 35.5 | 42.4 (25.4) * | 32.1 |
| **4** | 37.6 | 49.6 (42.8) * | 31.6 |
| **7** | 42.4 | 60.8 (59.9) * | 36.1 |
| **9** | 42.5 | 69.4 (70.9) * | 38.7 |
| **11** | 39.2 | 67.6 (76.0) * | 37.6 |
| **Grain per cycle** | 1.7 | 6.6 | 1.9 |

* The values within parenthesis are the estimates of average heterosis (heterosis over mid parent).

Reciprocal full-sib recurrent selection for yield was carried out for 8 cycles in the maize population BS 10 and BS11. Yields of the selected versions of BS10 and BS11 increased at the rate of 7.9 and 1.6% respectively, per cycle of selection. This was associated with a significant reduction in stalk lodging and no change in maturity. The yield of the population cross increased by 6.7% per cycle, while average heterosis increased from 2.5% in cycle zero to 28.4% in cycle 8 (Table 9.6). The increased heterosis was concluded to be the consequence of an accumulation of favourable alleles with additive and dominance effects, and by the heterozygous condition of those loci for which genetic drift had caused fixation of recessive alleles in one of the parentals

**Table 9.6: Effects of 8cycles of reciprocal full-sib recurrent selection for yield in maize (based on Hallauer, 1991).**

| Selection cycle | | Grain yield (q/ha) | |
|---|---|---|---|
| | **BS10** | **B10 x BS11**<br><br>**(Population cross)** | **BS11** |
| **0** | 41.5 | 46.5(2.5) * | 49.2 |
| **2** | 43.8 | 57.2 (16.7) | 51.5 |
| **4** | 50.9 | 59.6 (16.5) | 48.6 |
| **8** | 51.3 | 74.6 (28.4) | 55.6 |
| **Grain per cycle** | **7.9** | **6.7** | **1.6** |

*** Figures within parenthesis are per cent values for average heterosis.**

populations. The increased yield of BS10 was explained to be due mainly to alleles with additive effects, while that of BS11 was said to be mainly due to alleles having dominant effects. In the above two studies, (1) the increase in the yield of the population cross was higher than those reported in other studies, (2) and the rates for half-sib and full-sib schemes were comparable. (3) in addition, important alleles with additive and nonadditive effects were included in selection, and the importance of the two types of effects may differ between populations. Reciprocal recurrent selection methods should be an important component of maize germplasm improvement programmes, but they are not used as frequently as intrapopulation selection methods because they seem more complex. But in reality, reciprocal recurrent selection is no more complex or resource demanding than half-sib recurrent selection in the two populations separately (for comparison with reciprocal half-sib recurrent selection) or full-sib recurrent selection in one population (for comparison with reciprocal full-sib recurrent selection). Initially, intrapopulation selection methods are appropriate for certain specific traits, e.g., pest resistance, stalk strength, etc., but reciprocal recurrent selection improves established heterotic groups in the long-term.

The results from different selection scheme (table 20.3) are not strictly comparable with each other for the following reasons. (i) The different schemes were applied to different populations, and the response to selection may vary greatly from one population to another. (ii) The selection and evaluations were made during different years and at different locations. Thus, the E and G x E components of variation will be different for the different studies. (iii) The intensities of selection were different in many of these studies, and the effectiveness of selection is greatly affected by the selection intensity. Hence, the results from different selection studies should be compared with considerable caution.

The improved populations resulting from various selection schemes are excellent sources of good inbred lines; such populations may be expected to become increasingly important in the future. For example, the most important maize inbreds developed so far, namely, B73 was derives from an improved version of Stiff Stalk Synthetic. In conclusion, both theoretical consideration and practical experience underline the importance of improving the source population used for inbred development.

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