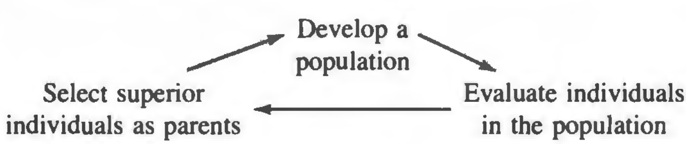
CHAPTER FIFTEEN

Recurrent Selection

Recurrent selection can be broadly defined as the systematic selection of desirable individuals from a population followed by recombination of the selected individuals to form a new population. The process can be envisioned as a circle that includes population development, evaluation of individuals, and selection of superior individuals as parents to form a new population for the next cycle of selection.



A cycle of selection is completed each time a new population has been formed. The initial population that is developed for a recurrent selection program is referred to as the base population or cycle 0 population. The population formed after one cycle of selection is called the cycle 1 population; the cycle 2 population is developed from the second cycle of selection, and so forth.

The process of recombination, evaluation, and selection occurs routinely in cultivar development programs. For example, the hybridization of elite inbred lines to form single-cross populations, followed by inbreeding, evaluation, and selection of the progeny, could be considered a cycle in a long-term recurrent selection program. However, the term recurrent selection is most often applied to breeding schemes that involve well-defined reference populations and short-term cycles of selection.

The objective of recurrent selection is to improve the performance of populations for one or more characters. The improved populations can be used as a cultivar per se, as parents of a cultivar-cross hybrid, and as a source of superior individuals that can be used as inbred lines, pure-line cultivars, clonal cultivars, or parents of a synthetic.

Successful recurrent selection results in an improved population that is superior to the original population in mean performance and in the performance of the best individuals within it (Fig. 15-1). Ideally, the population will be improved without its genetic variability being reduced so that additional selection and improvement can occur in the future.

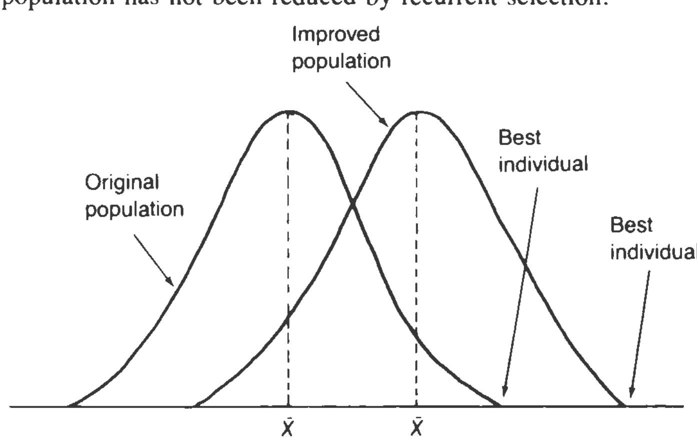
DEVELOPMENT OF BASE POPULATIONS

One consideration in developing a base population is that the parents should have the best performance possible for the characters to be improved through recurrent selection. Another important factor is that the parents should represent an array of different ancestries as a means of maximizing genetic diversity. The two criteria are not always possible to achieve, because potential parents with the best performance may be closely related.

A second consideration is the number of parents that should be used to form the cycle 0 population. The principle is to use as many parents as possible without unnecessarily sacrificing good performance for the characters of interest. The probability of having different alleles present in a population increases with the number of parents and with genetic diversity of the parents. Effective recurrent selection requires a high level of genetic variability in the population for the characters of interest.

A third consideration in the formation of a base population is the number of generations of intermating to conduct in developing the population. Each generation of intermating will improve the opportunity for recombination of genes

Figure 15-1 An idealized example of progress from recurrent selection. The improved population has a higher mean performance than and contains individuals superior to those in the original population. Genetic variability in the improved population has not been reduced by recurrent selection.



from the parents. Additional resources and time are required for each generation of intermating.

Recurrent selection can be conducted for the improvement of a single population (intrapopulation improvement) or for the simultaneous improvement of two populations (interpopulation improvement). The two populations used for interpopulation improvement should display a high level of heterosis for the character of interest when they are crossed together.

EVALUATION OF INDIVIDUALS IN THE POPULATION

Individuals in a population can be evaluated on the basis of their phenotype or on the basis of the performance of their progeny. The methods of intrapopulation improvement can be summarized as follows:

Phenotypic evaluation	*Genotypic evaluation*
Individual plant	Half-sib progeny
Clonal evaluation	Full-sib progeny
	Selfed progeny

Interpopulation improvement involves either half-sib or full-sib progeny evaluation.

Phenotypic evaluation can be based on an individual plant or the vegetatively propagated progeny of the plant in single or replicated plots. The evaluation can be made by visual inspection or by measuring the character of interest.

An individual plant can be evaluated by the performance of its progeny, commonly referred to as a family. The terms half-sib and full-sib refer to the genetic relationship among families, not to the individuals within a family. Half-sib families are formed by crossing a series of individuals to one common parent, which is referred to as the tester. Full-sib families are formed by crossing pairs of plants together. Half-sib families are related because they have a common parent, but full-sib families have no parents in common.

METHODS OF INTRAPOPULATION IMPROVEMENT

Recurrent Phenotypic Selection

Cyclic selection in a cross-pollinated population based on the phenotype of an individual plant has been referred to as mass selection, recurrent phenotypic selection, phenotypic recurrent selection, simple recurrent selection, and directed mass selection. The terms tend to be used interchangeably today; however, some people prefer to differentiate between mass selection and the other terms referring to recurrent selection. They refer to mass selection when female plants are selected after they have been pollinated by selected and unselected males in the population. They use the term recurrent phenotypic selection when the male and female parents are both controlled because only selected plants are intercrossed to obtain seed for the next cycle of selection. In this chapter, recurrent phenotypic selection will refer to phenotypic selection among individuals, regardless of the parental control involved.

Phenotypic selection of individual plants was the earliest method used to improve cross-pollinated species. In maize, farmers would annually select the most desirable ears in the field and use bulked seed from the selected ears to plant the next crop. Selection was based only on the female plant, because the ear was pollinated by both selected and unselected plants. The independent selection by farmers resulted in an array of open-pollinated cultivars that were genetically different.

Recurrent selection on the basis of individual plants that had been open-pollinated has been used in forages to improve populations. Law and Anderson (1940) conducted five cycles of selection for increased leafiness, number of culms, and basal diameter, and decreased plant height among open-pollinated plants of a big bluestem population. Leaf area of individual plants in the first season of plant growth after establishment increased from 1296 to 10,095 sq cm, number of culms increased from 57 to 148, plant height decreased from 132 to 76 cm, and basal diameter increased significantly.

In 1950, there were reports of recurrent selection in side-oats grama and maize based on individual plant performance, in which only selected individuals were recombined for the next cycle of selection. Harlan (1950) began a selection program in 1943 to increase the uniformity of side-oats grama for 18 different plant types, each selected independently in separate subpopulations. The cycle 0 population consisted of seed lots obtained from locations in Arizona, Kansas, Oklahoma, and Texas. He selected 14 plants of each of the 18 different plant types. The selected plants were transplanted to separate isolation blocks and allowed to open-pollinate. Seed was harvested from each block, and a population of approximately 180 individuals was established from each of the 18 subpopulations. Reselection for type was made in each of the subpopulations to form the cycle 2 populations. The recurrent selection practiced by Harlan involved control of both the male and female parents, because only selected plants were intercrossed to form the new population. This was done because he had noted from previous experience that selection was not effective when only the female parent was controlled. Harlan did not use the words mass selection or recurrent selection in discussing his work.

The research of Sprague and Brimhall (1950) in maize illustrated the marked effect that recurrent selection could have on the improvement of a population. The selection by these investigators was based on the phenotype (oil content) of selfed ears from individual plants. By using selfed seed from selected ears to form the new population, they controlled both the male and female parents. Their method of selection is outlined as follows. The genetic improvement of the population is illustrated in Fig. 15-2.

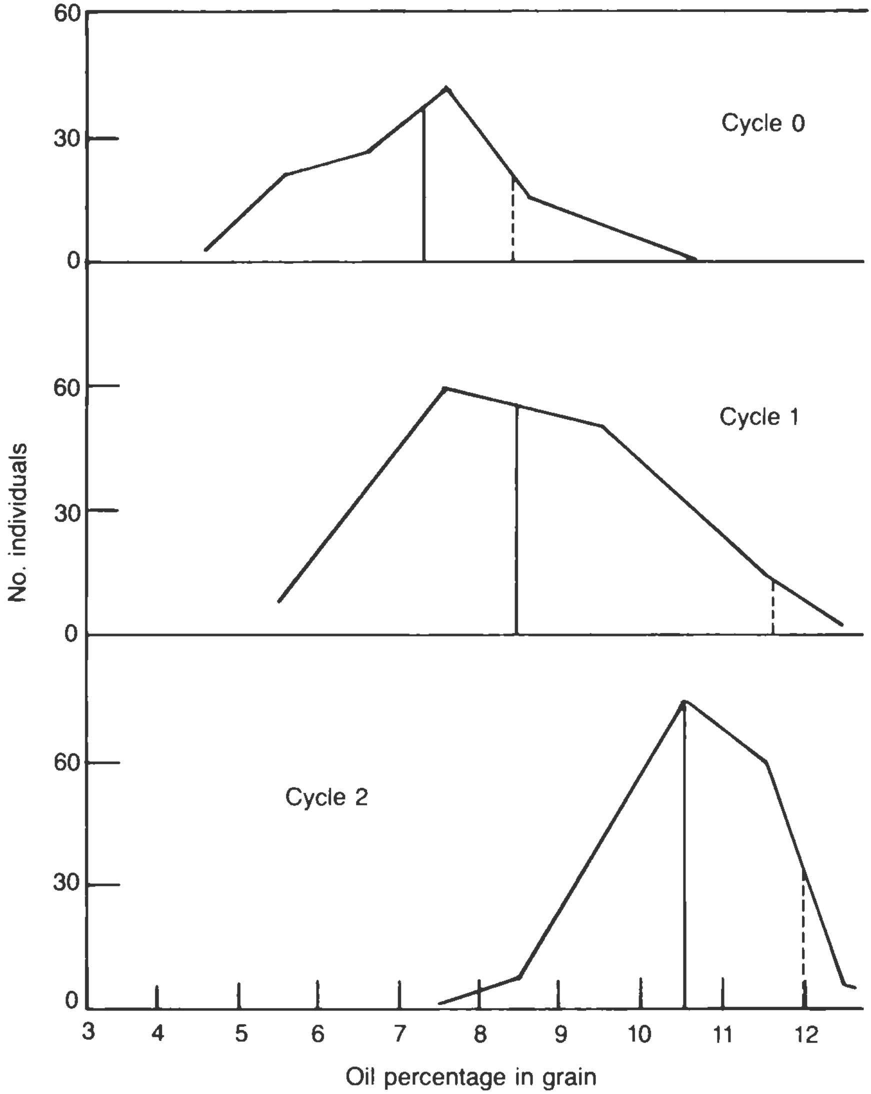


Figure 15-2 Frequency distributions for oil percentage in maize kernels of a population improved by recurrent selection. The solid vertical line in each distribution is the mean of the population, and the dotted vertical line is the mean of the selected individuals. (Adapted from Sprague and Brimhall, 1950.)

Season 1: Individual plants from a population (cycle 0) were self-pollinated. The ears from each plant were harvested separately and seeds from each plant were analyzed for oil percentage.

Season 2: Remnant selfed seeds from each plant selected for oil percentage were planted the following season and all possible intercrosses were made by hand. Equal quantities of seed from each cross were bulked to form the cycle 1 population.

Seasons 3 and 4: Seeds of the cycle 1 population were planted and the procedure used in seasons 1 and 2 was repeated to obtain the cycle 2 population. Subsequent cycles of selection would be conducted in the same manner.

The selection practiced by Harlan (1950) and by Sprague and Brimhall (1950) illustrates techniques for controlling both the female and male parent during recurrent phenotypic selection. Additional examples of selection procedures for control of both parents are provided by Jenkins and colleagues (1954), who selected for disease resistance before flowering in a maize population; by Graham and co-workers (1965), who selected for disease resistance in alfalfa; and by Bennett (1959), who selected for hard seededness in crimson clover.

Jenkins' selection procedure is as follows.

Season 1: The population for selection (cycle 0 population) was planted in the field. During June and July, the plants were inoculated six to eight times with a suspension of *Helminthosporium turcicum* cultures. At pollinating time, the most resistant plants were selected for interpollination. Pollen was collected from the resistant plants, mixed in approximately equal proportions, and placed on the silks of the resistant plants. Seed from the hand-pollinated ears was mixed in equal proportions to form the cycle 1 population for the next cycle of selection.

Season 2: The cycle 1 population was planted in the field and the procedure used in season 1 was repeated to obtain the cycle 2 population. Subsequent cycles of selection would be conducted in the same manner.

Graham's procedure is as follows.

Season 1: About 4900 seeds of a population (cycle 0) were sown in the greenhouse and plants were inoculated in a growth chamber with *Pseudopeziza medicaginis* when 25 to 35 days old. After 4 days in the chamber, plants were moved into the greenhouse. Three weeks after inoculation, disease ratings were made and about 150 plants rated as resistant were selected from the population and reinoculated to eliminate escapes. Approximately 85 plants rated as resistant after reinoculation were selected for intercrossing.

Season 2: The 85 resistant plants were intercrossed to obtain at least 5000 seeds of the cycle 1 population. The time required to complete one cycle of selection (seasons 1 and 2) was about six months.

Seasons 3 and 4: Seeds from the cycle 1 population would be planted and the procedure repeated as described for seasons 1 and 2 to obtain the cycle 2 population. Subsequent cycles of selection would be performed in the same manner.

Bennett's procedure is as follows.

Season 1: One hundred twenty pounds of composited crimson clover seeds from 42 sources (cycle 0 population) were evaluated for hard seed. The seeds were soaked in water for three days. The soaked seeds were rubbed between the hands and broken and swollen seed were floated off with water. The hard seeds were planted in the field, where open-pollination occurred. The seeds were hand threshed and bulked to form the cycle 1 population.

Season 2: One hundred pounds of seeds from the cycle 1 population were soaked for three days. Hard seeds obtained in the same manner as in season 1 were planted in the field. Open-pollinated seed harvested from the planting formed the cycle 2 population. Subsequent cycles of selection would be conducted in the same manner.

The term phenotypic recurrent selection was used by Johnson and El Banna (1957) to describe their selection program in sweetclover. They differentiated between genotypic and phenotypic recurrent selection. Genotypic recurrent selection referred to selection based on the combining ability of an individual, whereas phenotypic recurrent selection was based on the phenotype of the individual. They scored individual plants for growth habit and vigor, and intercrossed only selected individuals for the next cycle of selection. Dudley and colleagues (1963) used the term recurrent phenotypic selection in describing their program of individual plant selection in alfalfa. They used insects and hand pollination to intercross selected individuals.

The expected genetic gain from selection of only the female parent in a recurrent phenotypic selection program is one-half of the amount expected when both parents are selected (Chap. 2 and 17). For that reason, selection before pollination or the intercrossing of selected individuals that are propagated vegetatively or by selfed seed is preferred whenever it does not increase the length of time required to complete a cycle.

One of the problems with phenotypic selection of individual plants is the variability among plants caused by microenvironmental variation, i.e., differences among plants within a field caused by variation in soil type, fertility, moisture, and so forth. When plants are selected for yield, they might all come from one section of the field where the fertility is greatest, even though the individuals are not superior genetically. Gardner (1961) developed a procedure for reducing the effect of microenvironmental variation that involves subdividing a population of plants into blocks (Fig. 15-3, 15-4), sometimes referred to as gridding. His technique is as follows.

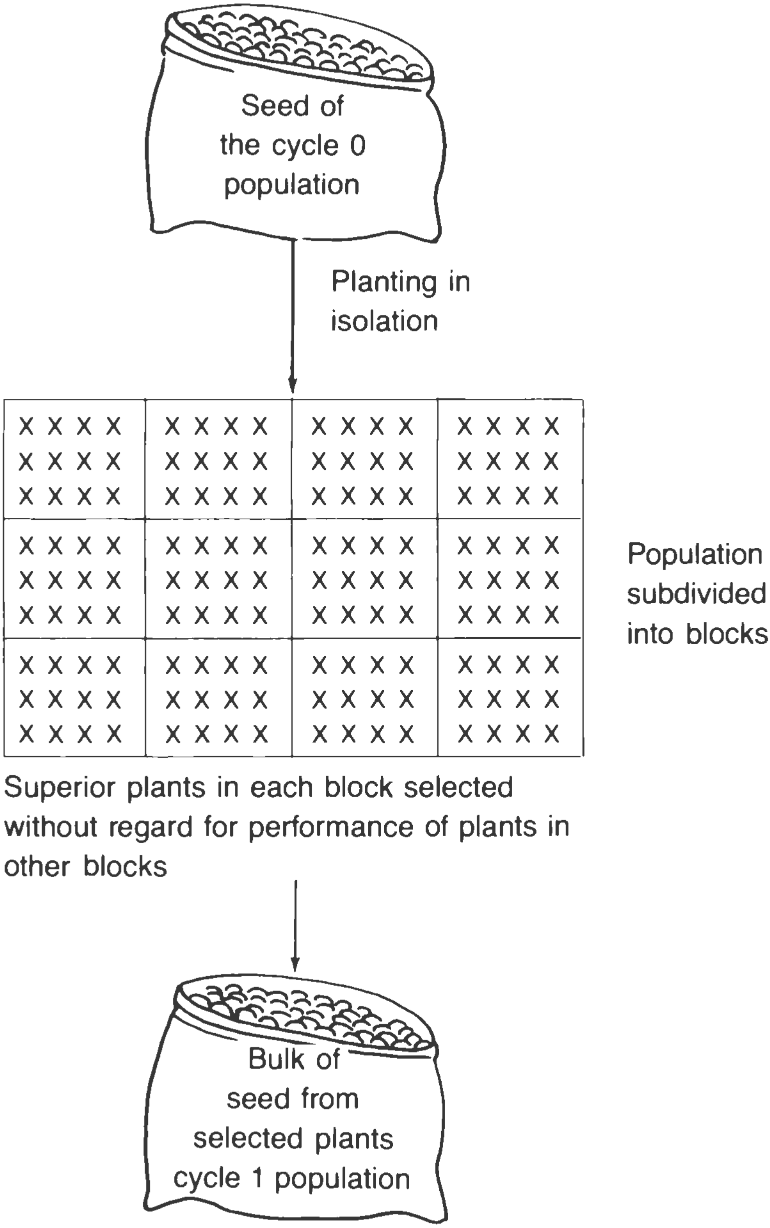


Figure 15-3 The effect of microenvironmental variability on recurrent phenotypic selection can be reduced by subdividing the population (cycle 0) of individual plants into blocks of a grid, selecting the superior individual within each block, and bulking the seed of selected individuals to form the new population (cycle 1) for the next cycle of selection (Gardner, 1961).

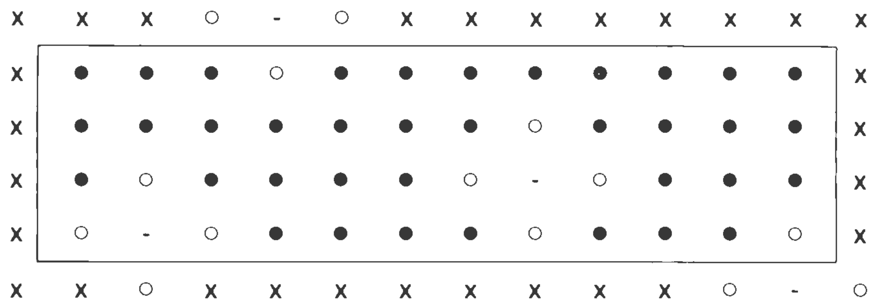


Figure 15-4 One block of a population of individual plants that has been subdivided by gridding to facilitate recurrent phenotypic selection. Only plants • that have competition on all sides are considered for selection. Missing plants are designated with a – and plants without adequate competition are indicated by o. Plants in adjacent blocks are indicated by x (Gardner, 1961).

Season 1: A nursery of approximately one-fifth hectare is planted with a random-mating population (cycle 0) in an area isolated from other maize. The seeds are planted in hills with 102 cm between rows and 51 cm between hills within the rows (19,370 hills/ha). To obtain uniform competition between plants, two seeds are planted in each hill and the hills are thinned to one plant shortly after plant emergence. If a hill has no plants, remnant seed of the population is planted in the hill and later the hill is thinned to one plant. Special care is taken at planting to place the seed at uniform depth so that seedlings do not emerge sporadically.

The isolation block is irrigated as needed during the growing season to avoid severe drought. All cultural practices (fertilization, cultivation, etc.) in the isolation nursery are done uniformly to avoid unequal treatment of the plants.

Before the time of selection, the field is divided into blocks of 40 competitive plants. A competitive plant is bordered by adjacent plants 51 cm apart within the row and 102 cm between rows. A block is generally four rows (four hills) wide and 10 hills (within the row) long. If the block does not contain 40 competitive plants, it can be extended to 11 or more hills within the four rows. There are 100 blocks of 40 plants within the isolation nursery.

At harvest, the best five to eight plants from each block are visually selected for yield potential. A lodged plant is considered one of the 40 competitive plants in a block. Seeds (ears) from each selected plant are bagged individually and the five to eight bags (plants) from each block are kept together in a larger sack. The seed is dried to a uniform moisture, shelled, and weighed. Twenty-five seeds from the four highest-yielding plants (10% selection intensity) in each block are bulked together (cycle

1 population) to plant the next cycle of selection. Twenty-five seeds from each of four plants in each of 100 blocks results in a 10,000-seed bulk. A similar bulk of 10,000 seeds is saved in case replanting is needed in the next cycle of selection.

Season 2: Seeds from the cycle 1 population are planted in the field and the procedure repeated as in season 1 to obtain the cycle 2 population. Subsequent cycles are conducted in the same manner.

Gardner's concept of stratifying a field for individual plant selection was one of the restrictions used by Burton (1974) in selecting for forage yield of Pensacola bahiagrass. He used the term recurrent restricted phenotypic selection to describe his procedure because he imposed five restrictions on selection among individual plants:

1. The space-planted population was divided into 25-plant square plots in a grid arrangement and the five highest yielding plants in each 25-plant plot were selected, as proposed by Gardner (1961).
2. Only the selected individuals were intercrossed to form the new population.
3. To facilitate intercrossing among selected individuals, two culms with heads ready to flower from each selected phenotype were placed together in water in the laboratory and the collection of flowering heads was agitated each morning to ensure maximum cross-pollination between all selected plants.
4. The use of two heads from each selected phenotype provided equal representation of the parents in the next cycle.
5. The choice of germplasm with a high degree of self-incompatibility reduced the likelihood of selfing of the parents.

Burton's restrictions demonstrate the degree of precision that can be developed for individual plant selection.

Recurrent Half-Sib Selection

Recurrent half-sib selection is a method of intrapopulation improvement that involves the evaluation of individuals through the use of their half-sib progeny. The general procedure for a cycle of selection is to cross the plants being evaluated to a common tester, evaluate the half-sib progeny from each plant, and intercross the selected individuals to form a new population.

There are many alternative procedures for conducting recurrent half-sib selection. The procedures differ by the testers used, the selection of one or both parents, and the seed used for intercrossing. The alternative procedures can be summarized as follows.

Alternative procedures for recurrent half-sib selection.

Tester	Parents Selected	Used for Intercrossing
Population	Female	Half-sib seed
Population	Male and female	Half-sib seed
Population	Male and female	Selfed seed or clones
Outside	Male and female	Selfed seed or clones

An outside tester refers to any germplasm other than the population being improved, such as inbred lines, single crosses, double crosses, and other populations.

The earliest form of recurrent half-sib selection was ear-to-row selection, described by a chemist, C. G. Hopkins, as a method of altering the chemical composition of maize (Hopkins, 1899). His selection work for chemical composition began with the 1896 crop of the open-pollinated maize cultivar 'Burr's White.' It marked the beginning of the long-term Illinois study of selection for seed composition in maize, which has undergone over 70 cycles of selection and is still in progress (Dudley, 1977).

The ear-to-row procedure as described by Hopkins involved the use of the population as the tester, and selection was based on unreplicated tests of the half-sib families in one environment. Because the plants chosen within selected families had been open-pollinated by selected and unselected individuals, only the female parent was selected.

A second procedure for improving open-pollinated maize cultivars by recurrent half-sib selection was proposed by Jenkins (1940). It was based on his observation that the general combining ability of an inbred line could be determined in early generations of inbreeding. The procedure involved the use of the population as the tester, selection of superior half-sib families based on replicated tests, and the use of selfed seed for intercrossing selected individuals.

A third procedure for recurrent half-sib selection was proposed by Hull (1945). The primary difference in Hull's procedure compared with that of Jenkins (1940) is the use of an inbred tester (Fig. 15–7). Hull referred to his procedure as recurrent selection for specific combining ability, because the objective was to develop an improved population or inbred lines from it that could be crossed with the tester to produce commercial seed. The work of Hopkins (1899), Jenkins (1940), and Hull (1945) formed the foundation for the alternative procedures of recurrent half-sib selection.

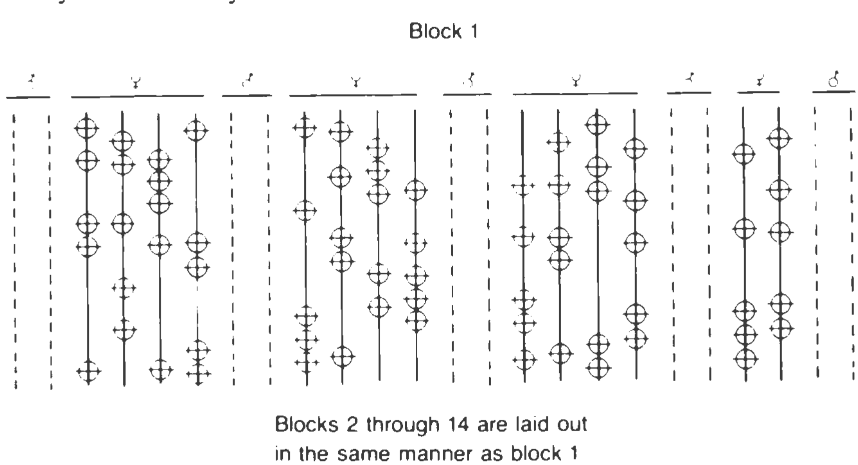
The procedures of recurrent half-sib selection that are available will be reviewed here on the basis of type of tester, parental control, and type of seed used for intercrossing. Alternative strategies within each of the categories will be considered.

Population as Tester, Female Parent Selected, Half-Sib Seed Used for Intercrossing. Ear-to-row selection as described by Hopkins (1899) was based on evaluation of half-sib families in unreplicated plots in one environment. His procedure did not provide information on the relative performance of families under different environmental conditions. To overcome this weakness, Lonnquist (1964) proposed that half-sib families be evaluated at multiple locations and that selection of plants within superior families be conducted in one replication planted in isolation. The procedure is referred to as modified ear-to-row selection because it was developed for use in maize; however, the method can be used in other species in which open-pollinated populations are available. One cycle of selection is completed each season.

Seeds (ears) are harvested from each of 190 plants in a random-mating population (cycle 0). Each of the 190 plants is a separate entry in the yield test of season 1.

Season 1: Six check entries and half-sib seed of the 190 plants are evaluated for yield and other characters. The six checks, consisting of the cycle 0 population and five hybrids, are included each cycle to measure progress from selection. The 196 entries are evaluated in a 14 × 14 triple lattice design with one replication planted at each of three locations. Each plot is a single row eight hills long. Standard techniques for yield evaluation

Figure 15-5 Plot arrangement in one replication of a 14 × 14 triple lattice design for the modified ear-to-row method of recurrent selection for seed yield in maize, as described by Lonnquist (1964). The female rows (half-sib families that are being evaluated for yield) are detasseled. The male rows are a bulk of seed from all the half-sib families in the test. Open-pollinated plants selected within each family are represented by ⊕, each of which is a potential half-sib family for the next cycle of selection.



are used, including planting of excess seed and thinning to the desired stand.

At one location, open-pollinated half-sib seed is obtained for the next cycle of selection (cycle 1 population) by planting the replication in isolation and including male rows for pollination (Fig. 15–5). Each block of the lattice at the location has four plots of the half-sib families alternating with two rows of the male parent. The male parent is a composite of an equal number of seeds from each of the 190 ears (half-sib families). The female rows, including the check entries, are detasseled before pollen shed.

The plots at the two locations that do not involve the special crossing arrangement are evaluated for important characters, and are harvested for yield in the usual way by threshing seed from all plants of a plot in bulk.

At the location where the entries have been detasseled, five plants with the best appearance in each of the 190 rows of half-sib families are marked before harvest by spraying red paint on the tip of their ears. The rows are harvested by hand, the ears from all plants in the row are weighed to determine yield, and the five marked ears are saved for each row.

The data for yield and other characters are summarized for the three locations and the top 20% of the 190 half-sib families (38) are selected. The five marked ears from the 38 selected families constitute the cycle 1 population. Seed from each ear will be a separate half-sib family in the next cycle of selection in season 2.

Season 2: The next cycle of selection is conducted in the manner described for season 1.

Alterations can be made in Lonnquist's procedure. The testing of half-sib families is not restricted to a triple lattice. A randomized complete-block or other experimental design also can be used. The half-sib families can be tested in more than one replication per location and at any number of locations. The number of half-sib families that are evaluated is not limited to any particular number.

Population as Tester, Male and Female Selected, Half-Sib Seed Used for Intercrossing. Selection of both the male and female parents involves the intercrossing of only selected half-sib families (Fig. 15-6). The genetic gain from controlling both parents is twice that expected when only the female parent is selected, but two seasons are required to complete a cycle of selection.

Seeds are harvested from plants in an intermated population (cycle 0). Half-sib progeny from each of the plants will be a separate entry in the replicated tests of season 1. Part of the half-sib seed from each plant is put in storage for potential use in crossing during season 2.

Season 1: The half-sib families are evaluated in replicated tests at several locations, and the superior half-sib families are selected for crossing in season 2.

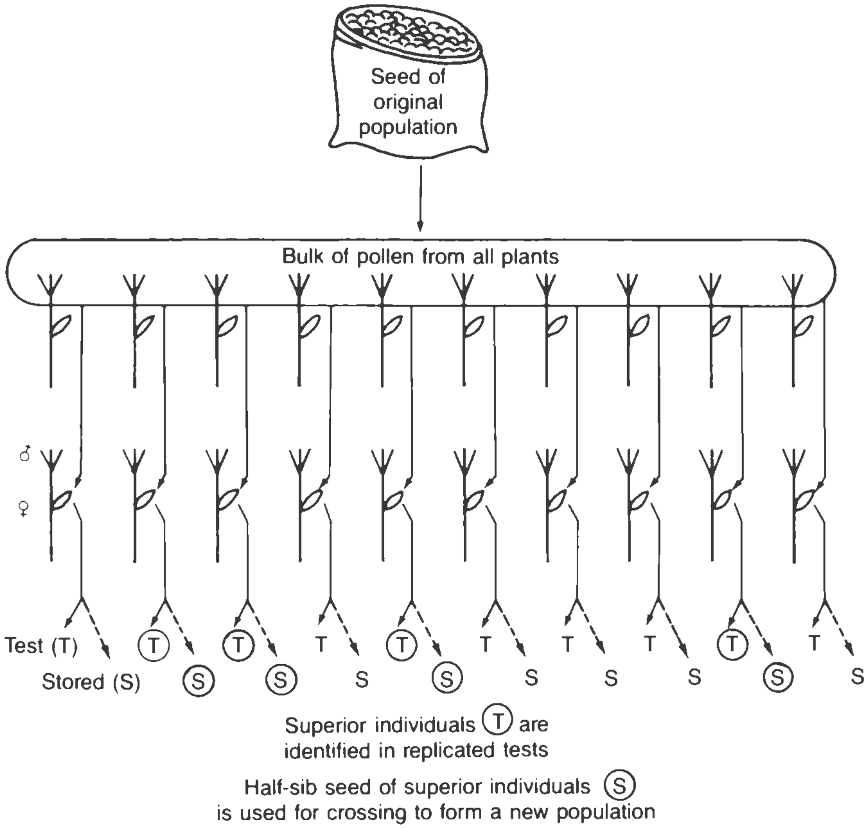


Figure 15-6 Intrapopulation improvement by recurrent selection among half-sib families when the population is used as the tester. Part of the half-sib seed produced on each individual is used for replicated tests and the other part is stored for use in forming the new population.

Season 2: Remnant half-sib seed of selected individuals is used for crossing to form new half-sib families of the cycle 1 population. Part of the half-sib seed produced on each plant is used for replicated tests in season 3 and part is put in storage for potential use in crossing during season 4.

Seasons 3 to 4: The second cycle of selection is conducted by repeating the procedures used in seasons 1 and 2. Subsequent cycles of selection are conducted in the same manner.

Selection can be practiced within half-sib families to increase the genetic gain per cycle. Compton and Comstock (1976) suggested an alteration of Lonnquist's modified ear-to-row selection that permitted selection of both parents and selection within the chosen half-sib families. The procedure requires two seasons per cycle, both of which are suitable for selection of the character of interest.

Seeds are harvested from plants in an intermated population (cycle 0). Half-sib progeny from each of the plants will be a separate entry in the yield test of season 1. Part of the half-sib seed from each plant is put in storage for use in intercrossing during season 2.

Season 1: The half sib families and appropriate checks are evaluated for yield and other characters in replicated tests at several locations. The superior half-sib families are selected for intercrossing in season 2.

Season 2: To permit both selection and intercrossing during season 2, the environment must be one to which the lines are adapted. This prevents the use of some winter nurseries that are suitable for intercrossing but where selection for yield and other important characters is not possible because conditions are not representative of the area in which the lines normally would be grown.

Remnant half-sib seed of the selected half-sib families is taken from storage and a crossing block is planted in isolation. Rows of the half-sib families used as females are alternated with rows of the male parent in an appropriate ratio. The male parent is a composite of an equal number of seeds from each of the selected half-sib families. Standard plot techniques are used to permit visual selection for yield and other characters.

The female rows are detasseled before pollen shed. Within each female row, ears from the five plants that have the best appearance are harvested. The five selected plants from each half-sib family constitute the entries from the cycle 1 population that will be evaluated in the next cycle of selection. Part of the half-sib seed from each plant is used to evaluate the half-sib families in season 3 and part is put in storage to be used for intercrossing selected families in season 4.

Seasons 3 and 4: The second cycle of selection is conducted. Each cycle is conducted in the manner described for seasons 1 and 2.

Population as Tester, Male and Female Parents Selected, Selfed Seed or Clones Used for Intercrossing. The genetic improvement per cycle from half-sib evaluation can be enhanced by the use of selfed seed or clones from selected individuals to form the new population, rather than the use of remnant half-sib seed (Fig. 15–7). The increased gain with the use of selfed seed or clones is due to greater parental control over the alleles that are transferred to the new population (Chap. 17). When half-sib seed is produced, individuals in the population receive half of their alleles from the male parent. Some of the male gametes have favorable alleles for the character under selection, and other gametes have unfavorable alleles. When half-sib seed from selected individuals is used for intercrossing, the unfavorable alleles of the male gametes reduce the amount of genetic improvement in the population. When selfed seed or clones are used to form the new population, only gametes from the selected individuals are passed to the new population, not the unfavorable male gametes used to produce half-sib seed for testing.

Season 1: Plants from an intermated population (cycle 0) are manually self-pollinated and crossed to the tester. For vegetatively propagated species, half-sib seed is obtained on plants by open-pollination. The selfed seed is stored or the clones are maintained for intercrossing selected individuals in season 3. The half-sib seed is used for testing in season 2.

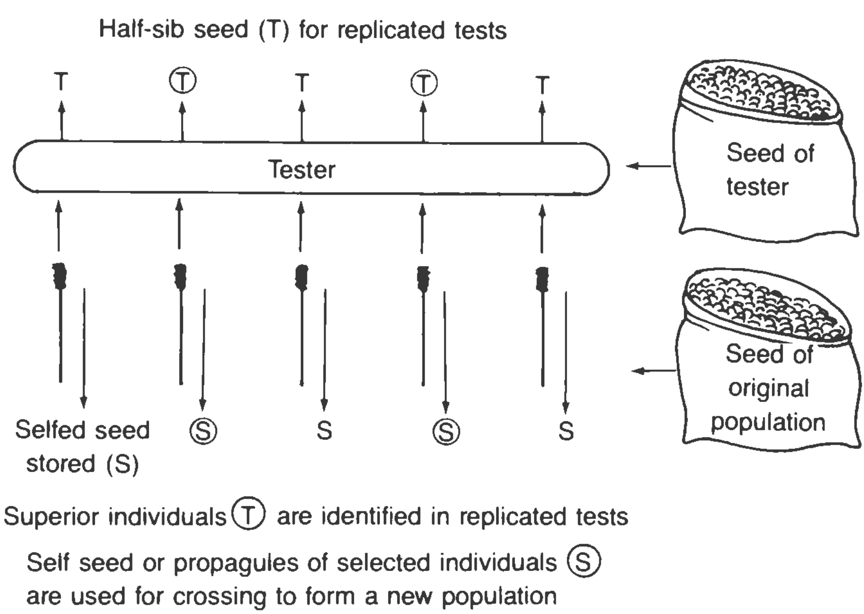
Season 2: The half-sib families are evaluated in replicated tests and the superior ones are selected.

Season 3: Selfed seed or clones from plants that produced selected half-sib families are used for intercrossing to form the cycle 1 population.

Seasons 4 to 6: The second cycle of selection is conducted. The procedure for seasons 1 through 3 is repeated for each cycle of selection.

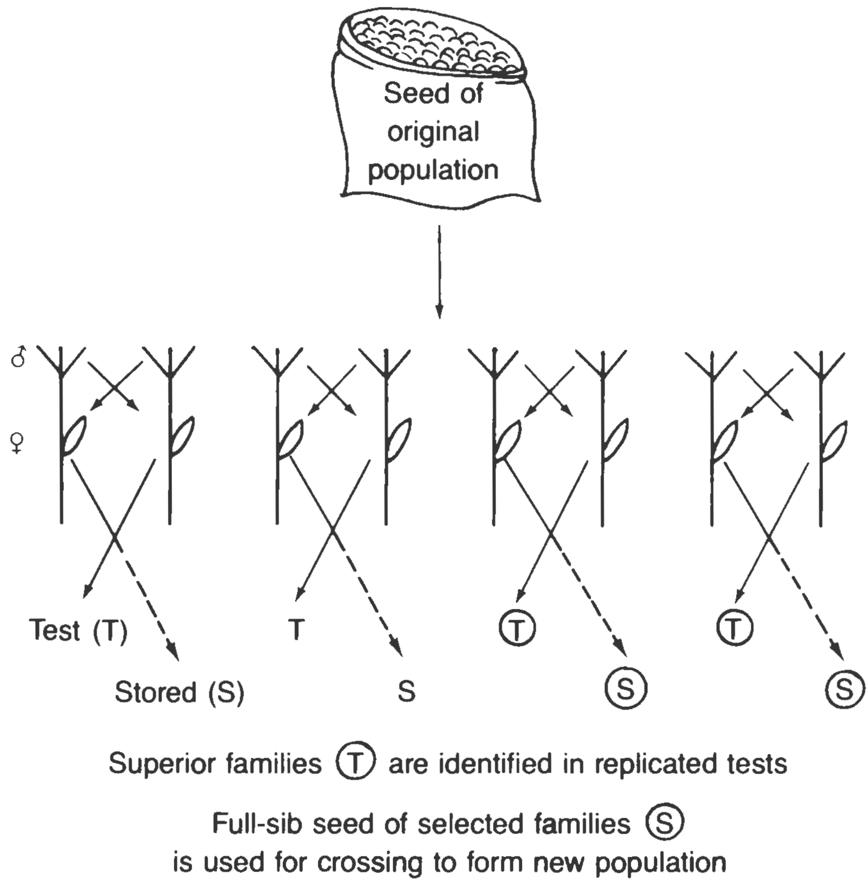
Although the use of selfed seed or clones can increase genetic gain per cycle compared with use of half-sib seed, the genetic gain per year may be less because one extra season is required for recombination. Consequently, the choice between the two procedures will depend in part on the number and types of seasons available to the breeder (Chap. 17).

Figure 15-7 Intrapopulation improvement by recurrent selection among half-sib families when the population is not the tester. Pollen from the test individual is used to pollinate several individuals of the tester to obtain the half-sib seed needed for replicated tests. After superior individuals are identified, selfed seed or vegetative propagules are used for crossing to form the new population.



Tester Other Than the Population, Male and Female Parents Selected, Selfed Seed or Clones Used for Intercrossing. The steps for recurrent half-sib selection with a tester other than the population are the same as those outlined on page 187. The tester used to form the half-sib seed can be a homogeneous inbred line that produces gametes with the same genotype (Fig. 15-7). It also may be a cross or population that provides a heterogeneous array of gametes to the individuals that are to be evaluated. The choice of tester can influence the genetic gain per cycle (Chap. 17). When an inbred tester is used, genetic variability among families may be increased compared with use of the population per se as tester (Sprague and Eberhart, 1977).

Figure 15-8 Intrapopulation improvement by recurrent selection among full-sib families. Part of the full-sib seed produced from paired-plant crosses is used for replicated tests and the other part is stored for use in forming the new population.



RECURRENT FULL-SIB SELECTION

Recurrent full-sib selection is a method of intrapopulation improvement that involves the testing of paired-plant crosses (Fig. 15-8). It is the only method of recurrent selection in which the seeds from two individuals, rather than one, are used for testing and to form the new population.

Season 1: Full-sib families are developed by making crosses between pairs of selected plants in a population (cycle 0). Part of the full-sib seed is put in storage for use in intercrossing selected full-sib families in season 3. The other part of the seed is used for testing in season 2.

Season 2: The full-sib families are evaluated in replicated tests and the superior families are selected.

Season 3: Remnant full-sib seed is used to intercross the selected families. The intercrossed seed that is harvested (cycle 1) is used to begin the next cycle of selection.

Seasons 4 to 6: The second cycle of selection is conducted by repeating the procedures used in seasons 1 to 3. Subsequent cycles of selection are conducted in the same manner.

There are two basic alternatives for the formation of new full-sib families between cycles of selection. One procedure is to cross the selected families and obtain S_0 seed in one season, followed by paired-plant crosses to form full-sib families during the next season as described above. The second procedure is to form new full-sib families in a single season of crossing, thereby reducing the number of seasons per cycle (Hallauer and Miranda, 1981). In the second procedure, full-sib seeds of each of the selected families would be planted in separate rows. Plants from different rows (families) would be paired to obtain the new full-sib families. This modification would permit a cycle of selection in two seasons, but would reduce the amount of recombination between cycles of selection.

RECURRENT SELECTION AMONG SELFED FAMILIES

Recurrent selection among progeny of self-pollinated plants is a method of intrapopulation improvement that is used in both self- and cross-pollinated crops. It involves the testing of lines after one or more generations of selfing followed by intercrossing of individuals to form the new population.

$S_{0:1}$ lines are commonly used for recurrent selection (Fig. 15-9):

Season 1: S_0 plants from an intermated population (cycle 0) are self-pollinated and harvested individually. Part of the S_1 seed from each plant is stored for use in intercrossing selected lines in season 3 and part is used for testing in season 2.

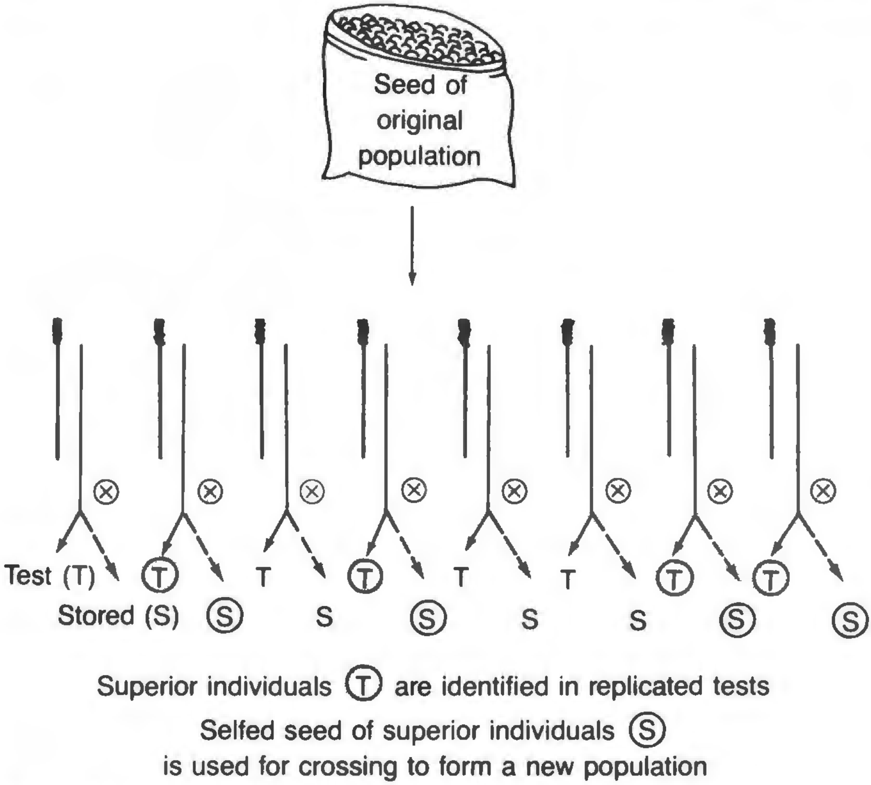


Figure 15-9 Intrapopulation improvement by recurrent selection among $S_{0:1}$ lines. Part of the selfed seed produced on each individual is used for replicated tests and the other part is stored for use in forming the new population.

Season 2: The $S_{0:1}$ lines are evaluated in replicated tests and the superior lines are selected.

Season 3: Remnant S_1 seed is used to intercross the selected lines. The S_0 seed obtained from the crosses represents the cycle 1 population.

Season 4: The next cycle begins. The procedure of seasons 1 to 3 is used for each cycle of selection.

The procedure used to test lines in more advanced generations of self-pollination can be outlined with evaluation of $S_{1:2}$ lines:

Season 1: An intermated population (cycle 0) is planted and selected S_0 plants are self-pollinated manually or naturally. The procedure for seed harvest will depend on the method chosen to maintain the population during selfing (the single-hill procedure of single-seed descent will be used for this example). S_1 seeds are harvested separately from each S_0 plant.

Season 2: Each $S_{0:1}$ line is planted in a separate hill. Plants are self-pollinated within each line, and S_2 seed is harvested from individual plants. Part of the S_2 seed is put in storage for use in intercrossing selected lines during season 4 and the other part is used for testing in season 3.

Season 3: The $S_{1:2}$ lines obtained in season 2 are evaluated in replicated tests and the superior lines are selected for intercrossing.

Season 4: Remnant S_2 seed is used to conduct the first generation of intermating among the lines selected in season 3.

Season 5: Hybrid seed from season 4 is used to conduct the second generation of intermating to obtain S_0 seeds of the cycle 1 population.

Season 6: The next cycle begins by planting the cycle 1 population. Each cycle is conducted by repeating the procedures used in seasons 1 to 5.

There are various ways to modify the procedures just outlined.

1. One season per cycle can be eliminated if lines can be selected and intercrossed the same season. As an example, the schedule for evaluation of $S_{0:1}$ lines would be to self and harvest S_0 plants in season 1 and to test, select, and intercross the $S_{0:1}$ lines in season 2. This can only be done for characters that are evaluated before flowering is completed.
2. The number of seasons per cycle must be increased if insufficient seed is obtained on a single plant to conduct the necessary replicated tests. In the additional season, a progeny row would be grown from each selected plant, a number of plants would be self-pollinated within each row, and bulk seed from the selfed plants in each row would be used for testing the following season. For example, the schedule might be to select S_0 plants in season 1, increase the seed of each $S_{0:1}$ line in season 2, test and select the $S_{0:2}$ lines in season 3, and intercross selected lines in season 4.
3. Sometimes seed from a selfed plant is insufficient for testing and to retain a sample in storage for subsequent intercrossing. In those instances, self-pollinated seed of each line must be increased the same season that replicated tests are being conducted. In a self-pollinated species, seed harvested from the replicated tests can be used if there is minimal outcrossing and the seed is not mixed during harvest. When outcrossing or seed mixtures can occur in the replicated tests, a separate planting is made of each line, plants within each line are self-pollinated, and selfed seed from within each row is bulked for use in intercrossing. When a seed increase is needed, S_2 seed would be used to intercross selected $S_{0:1}$ lines, S_3 seed would be used for $S_{1:2}$ lines, and so forth.
4. The number of seasons per cycle is directly related to the number of intermating generations that are used to develop the population for the next cycle of selection. One or more seasons may be used for intermating.
5. Selection can and should be practiced during any generation in which the lines are grown in a suitable environment. It is common to select among

S_0 plants before and after pollination, and to select among and within rows during subsequent generations of selfing.

METHODS OF INTERPOPULATION IMPROVEMENT

Reciprocal Half-Sib Selection

Reciprocal half-sib selection, also referred to as reciprocal recurrent selection, is a procedure of interpopulation improvement. It was proposed by Comstock and colleagues (1949) as a method for the simultaneous improvement of two populations (Fig. 15-10). Two segregating populations are selected, one of which can be designated A and the other B. Population A is used as the tester to evaluate individuals in population B, and vice versa:

Season 1: One-hundred plants selected in population A (cycle 0) are selfed and crossed to six or more random plants in population B. One-hundred plants selected in population B (cycle 0) are selfed and crossed to six or more random plants in population A. The selfed seed of each plant is put in storage. The half-sib seed is used for testing in season 2.

Season 2: A replicated test is conducted to evaluate the 100 half-sib families of population A and the 100 from population B. On the basis of test results, the top 10 half-sib families are selected from each population.

Season 3: The 10 plants in population A that had superior half-sib progeny performance in season 2 are intercrossed to form a cycle 1 population using the selfed seed produced in season 1. The 10 plants in population B that had superior half-sib progeny performance are intercrossed in the same manner to form a cycle 1 population.

Season 4: The cycle 1 seed of populations A and B are used to conduct the next cycle of selection in the same manner as that described for seasons 1 to 3.

Several modifications of this procedure have been suggested. Russell and Eberhart (1975) suggested a modification based on the consideration that the genetic variance among half-sib families is expected to increase when an inbred tester is used compared with the population as tester. In their procedure, individuals in population A would be selfed and crossed to an inbred line tester from population B that was derived from a previous cycle of selection. Similarly, individuals in population B would be selfed and crossed to an inbred line tester derived from population A. As the program progresses, a superior line from improved population A could become the new tester for population B, and a superior line from population B could become the new tester for population A.

Another modification of reciprocal half-sib selection was suggested by Paterniani (1967) to simplify the production of half-sib seed and to increase its quantity:

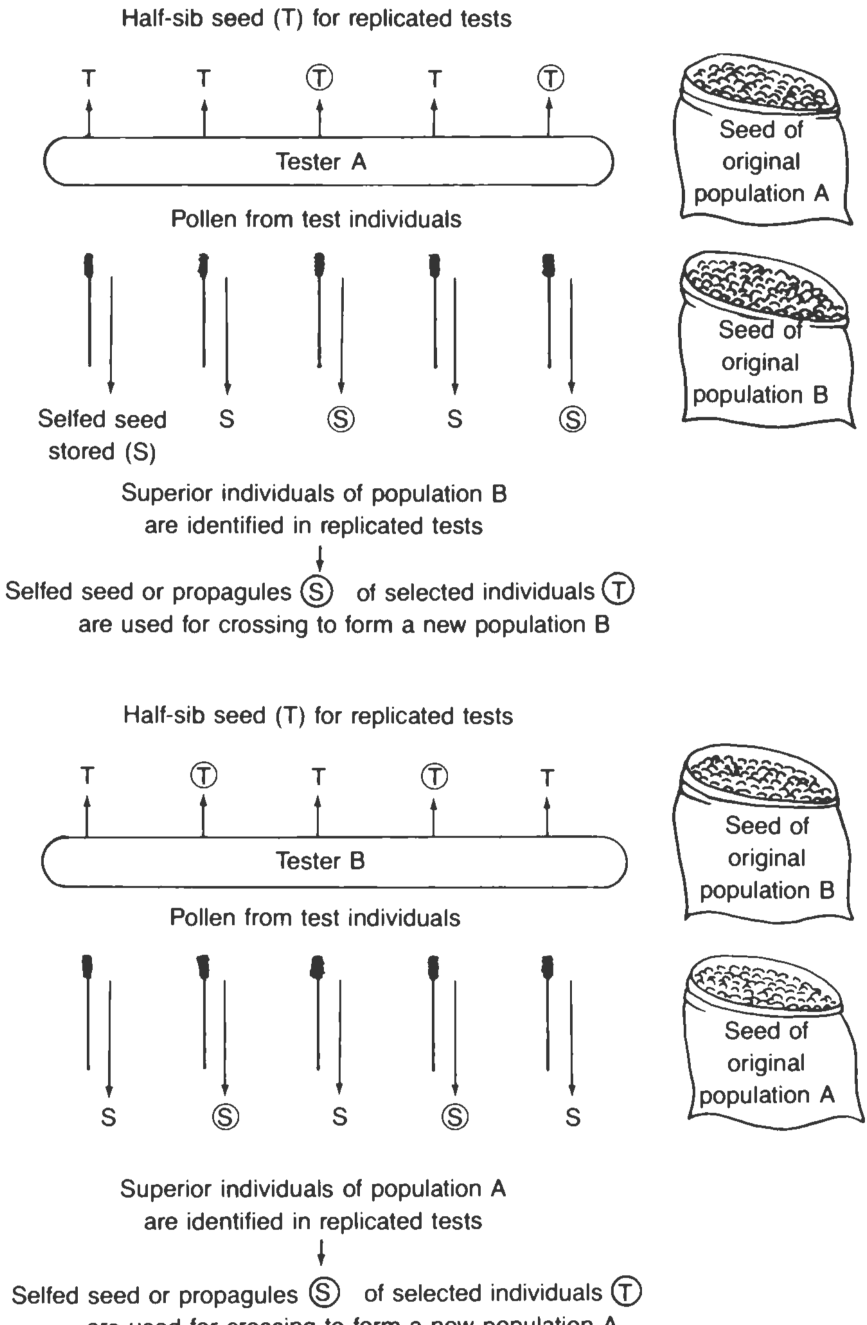


Figure 15-10 Interpopulation improvement by reciprocal half-sib selection. Population A is used as the tester for individuals of population B and vice versa to form half-sib families.

Seeds of population A (cycle 0) and population B (cycle 0) are planted in separate isolations and open-pollination is allowed to take place. Seed is harvested from 100 phenotypically desirable plants in population A and from 100 in population B. Part of the half-sib seed from each plant is retained in storage for use in intercrossing selected individuals in season 3. The other part of the seed is used to produce half-sib seed in season 1.

Season 1: Seed is planted from each of the 100 plants (half-sib families) of population A in separate rows to be used as female and from alternate rows of population B (cycle 0) to be used as male. The ratio of female to male rows will vary with the species. In the female rows, the source of male pollen is removed such as by detasseling in maize. The open-pollinated seed from the female rows is harvested for use in testing during season 2.

The same procedure is used in a separate isolation to obtain open-pollinated seed for the 100 plants (half-sib families) of population B.

Season 2: The seed produced in season 1 is used to evaluate in replicated tests the 100 half-sib families of population A and the 100 of population B. The superior 10 percent of the families in each population are selected.

Season 3: Remnant half-sib seed that had been placed in storage before season 1 is used to intercross the 10 individuals of population A that were found to be superior in season 2. The same is done for selected individuals in population B. The seed of selected lines is planted in isolation for each population, open-pollination is allowed to occur, and seed is harvested from 100 phenotypically desirable plants (cycle 1) to begin the next cycle of selection. Part of the half-sib seed from each plant is put in storage for use in intercrossing of selected individuals and part of the seed is used to produce half-sib seed as in season 1. The procedure of seasons 1 to 3 are repeated for each cycle of selection.

One major effect of Paterniani's procedure on genetic improvement per cycle relates to the use of half-sib seed of superior individuals to form the new population. By use of half-sib seed, the parental control is reduced by 50 percent compared with the use of selfed seed or vegetative propagules from selected individuals. Genetic improvement also is reduced by two seasons of crossing to obtain half-sib seed for testing. When an individual is crossed to the tester the first season, it contributes half of the alleles to the half-sib seed. Its genetic contribution to the half-sib seed used for testing is reduced to one-fourth when its half-sib progeny are crossed a second time to the tester. If each individual contributes such a small fraction of its alleles to the seed for testing, genetic differences among individuals may be minimal due to the masking effect of genes from the tester.

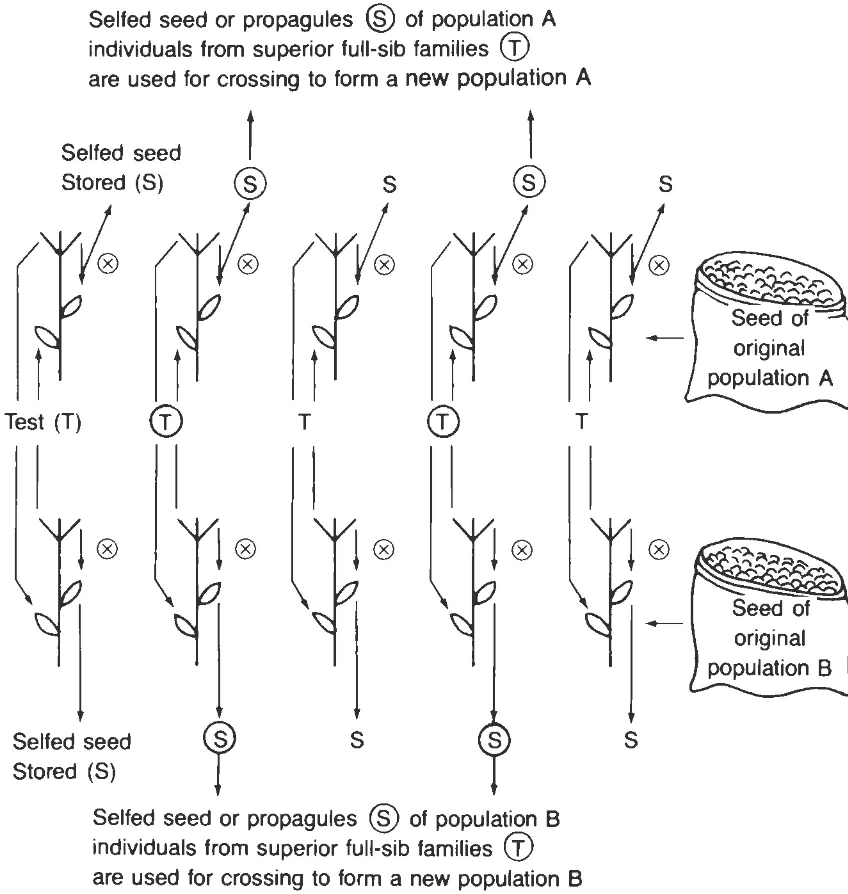


Figure 15-11 Interpopulation improvement by reciprocal full-sib selection. Paired-plant crosses between population A and population B form the full-sib families for evaluation in replicated tests.

Reciprocal Full-Sib Selection

Reciprocal full-sib selection is a method of interpopulation improvement for species in which the commercial product is hybrid seed (Fig. 15-11). It was described independently by maize breeders in Iowa and Nebraska (Hallauer, 1967a,b; Lonnquist and Williams, 1967). A cycle of selection is completed in the fewest number of seasons by the use of plants from which both selfed and hybrid seed can be obtained.

Season 1: Two hundred phenotypically desirable S_0 plants in population A (cycle 0) are paired with 200 plants in population B (cycle 0). For each of the pairs, the plants are selfed and crossed to the other member of the pair. If plants in only one population have the ability to produce both selfed and full-sib seed, the plants in that population must produce all the full-sib seed of the pair needed for testing.

Part of the selfed seed for each plant of a pair is put in storage to be used for intercrossing selected individuals in season 3. The other part of the seed can be used for continued selfing and selection for the development of inbred lines for use in producing commercial hybrids.

Hybrid (full-sib) seed from each pair is used for testing in season 2.

Season 2: The 200 full-sib families are evaluated in replicated tests and the superior 10 percent of the pairs are selected.

Season 3: Selfed seed from storage is used to intercross the 20 individuals of population A that were members of the 20 top full-sib families. Independently, selfed seed from storage is used to intercross the 20 individuals of population B that were members of the 20 top full-sib families. The intercrossed seed of populations A and B represent the cycle 1 populations.

Season 4: Two hundred phenotypically desirable S_0 plants in population A (cycle 1) are paired with 200 plants in population B (cycle 1). The procedure used in seasons 1 to 3 is repeated to obtain the cycle 2 populations. Subsequent cycles are conducted in the same manner.

Reciprocal full-sib selection can be used in species and populations in which selfed and hybrid seed cannot be obtained on the same plant, but the number of seasons per cycle is increased:

Season 1: Two hundred phenotypically desirable S_0 plants in population A (cycle 0) and 200 in population B (cycle 0) are self-pollinated. S_1 seed is harvested from each selected plant. Part of the S_1 seed can be put in storage for use in intercrossing selected individuals in season 4. The other part of the S_1 seed is used for season 2.

Season 2: Each $S_{0:1}$ line of population A is paired with an $S_{0:1}$ line in population B. Crosses are made between the members of each pair to obtain full-sib seed. Bulk pollen from plants in one line can be used to pollinate the other, and vice versa. The full-sib seed from the two members of each pair is bulked for use in testing during season 3.

Season 3: The 200 full-sib families are tested and the top 10 percent of the families are selected.

Season 4: Selfed seed from storage is used to intercross the 20 individuals of population A that were members of the top 20 full-sib families. Independently, selfed seed from storage is used to intercross the 20 individuals of population B that were members of the top 20 full-sib families.

The intercrossed seed of populations A and B represent the cycle 1 populations.

Season 5: Two hundred phenotypically desirable S_0 plants in population A (cycle 1) and 200 in population B (cycle 1) are selfed. The procedure used in seasons 1 to 4 is repeated to obtain the cycle 2 populations. Subsequent cycles are conducted in the same manner.

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