Population improvement was the earliest method applied to cross-pollinated crops. Mass selection has been used by farmers since early days and may be expected to have played a significant role in the improvement of cross-pollinated crops. The interest in population improvement methods declined with the development of hybrid and synthetic varieties. However, breeders are now paying increasingly more attention to population improvement programmes since the last four decades. The maize improvement programmes at CIMMYT, Mexico and the pearl millet improvement programme at ICRISAT, Hyderabad, are largely based on population improvement. The All India Coordinated Maize Improvement Project is placing an increasingly greater emphasis on population improvement.

21.2. METHODS OF POPULATION IMPROVEMENT

The various breedig methods used for population improvement may be grouped into the following two general classes: (1) methods without progeny testing and (2) methods with progeny testing. A more comprehensive and commonly used classification of selection schemes is presented in Table 21.1.

21.2.1. Breeding Methods Without Progeny Testing

In breeding methods belonging to this group, plants are selected on the basis of their phenotype, and no progeny test is carried out, *e.g.*, mass selection.

21.2.2. Breeding Methods With Progeny Testing

In most breeding methods, however, plants are initially selected on the basis of their phenotype, but the final selection of 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.

TABLE 21.1

A brief description of the various selection schemes for population improvement (the description is based primarily on maize)

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 comparison; 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 modified ear-to-row, but only superior progenies planted in the crossing block and allowed to open-pollinate.
d. Modified half-sib	Half-sibs used for yield trial: S_1 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 the 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 selection given 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 testcross progenies are evaluated in field trial. S_1 families of plants from A producing superior testcross progenies are intermated; the same is done for those from B. Requires at least two ears/plant in one of the two populations.

21.3. OBJECTIVES OF SELECTION

In self–pollinated crops, 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 self-pollinated crops are naturally homozygous and generally do not show appreciable inbreeding depression. In contrast, cross-pollinated crops generally show moderate to severe inbreeding depression. Consequently, (1) inbreeding must be avoided or kept to a minimum in cross-pollinated species. Further, (2) individual plants from such crops are highly heterozygous; the progeny from such plants 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 or genotypes. As a result, the phenotype of the population would be favourably changed in the direction of selection.

It should be clearly understood that in the case of cross-pollinated species, the genotype of the individual plants 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.

21.4. MASS SELECTION

Mass selection is the oldest breeding scheme available for cross-pollinated crops. *In **mass selection**, a number of plants are selected on the basis of 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 (usually about 10% in maize, *Z. mays*). Thus mass selection is based on the maternal parent only, and there is no control on the pollen parent. Selection of plants is based on their phenotype and no progeny test is conducted. Mass selection, as applied to cross-pollinated crops is essentially the same as that applied to self-pollinated crops; a generalised scheme for the method is outlined in Fig. 21.1. 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.* 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.

21.4.1. Merits of Mass Selection

1. Mass selection is an extremely simple breeding programme. Work of the breeder is kept to a minimum since selections is based on the phenotype of plants.
2. The selection cycle is very short, *i.e.*, of only one generation. Thus in every generation, one cycle of selection is completed.

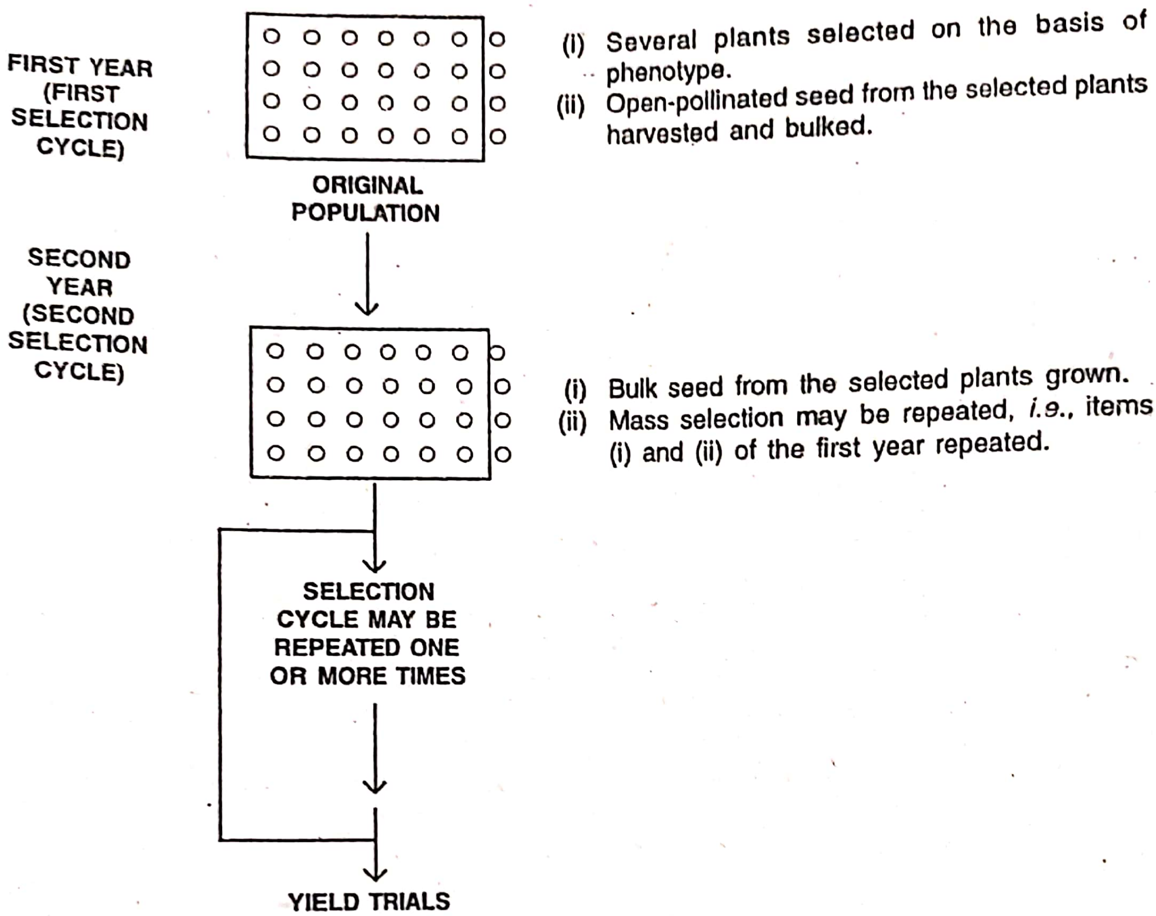

Fig. 21.1. Mass selection as applied to cross-pollinated crop species. When the selection is repeated one or more times, as outlined here, the scheme is known as *phenotypic recurrent selection.*

3. It is highly efficient in improving characters that are easily identified visually and have high heritability, *e.g.*, plant height, size of ear, date of maturity, etc.
4. If proper care is taken, mass selection is effective in improving yields of cross-pollinated crops. Most cross-pollinated crops have a high additive component of genetic variance, which responds to selection.
5. Since the improved strain is 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.

21.4.2. Demerits of Mass Selection

1. 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.
2. The selected plants are pollinated by both superior and inferior plants present in the population as the selected plants are allowed to open-pollinate. This reduces the effectiveness of selection.
3. High intensities of selection reduce population size and, as a result, lead to some inbreeding. Inbreeding depression may nullify the advances made under selection.

21.4.3. Modifications of Mass Selection

The two basic defects of mass selection, *viz.*, (*i*) lack of control of the pollen source and (2) the confusing effect of the environment on the phenotypes of individual plants, can be corrected by suitable modifications of the selection scheme; these modifications are briefly described below.

1. Inferior plants in the field are detasselled, and the remaining plants are allowed to open-pollinate. This modification exercises some control on the pollen source but the identification of inferior plants, of necessity, is based on only those characters, which are expressed before flowering.
2. Pollen from all the selected plants is collected and bulked; this pollen is used to pollinate the selected plants. This scheme ensures full control on the pollen source, but it can be applied to only those characters, which can be selected for before pollen shedding.
3. ***Stratified Mass Selection.*** This modification, suggested by Gardner in 1961, is also known as the ***grid method of mass selection.*** The field, from which selection is to be done, 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 the 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 increased yield has continued in Hays Golden even after 30 cycles of selection.
4. 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 minimise the environmental influence on the yields of plants being selected. It employs the principle of contiguous control discussed earlier in some detail (Chapter 16).

21.4.4. Effectiveness of Mass Selection

The results from selection studies using mass selection have been summarised by Hallauer and Miranda (1981). 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 blight, days to flowering (tasselling as well as silking), prolificacy and stalk volume, and in other crop species. Mass selection, particularly with stratification, has also been 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 summarised in Table 21.2. 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 as well. It is not surprising since polificacy 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 21.2

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	5.2 cm	2.5, 7.9 cm	
Decreased	6	4–12	3.5 cm	2.0–7.9 cm	2.0–3.2 cm
			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		

21.5. SELECTION SCHEMES WITH PROGENY TEST

21.5.1. Progeny Selection

The simplest form of progeny selection is the ***ear-to-row method,*** which has been extensively used in maize. This method was developed by Hopkins in 1908. In its simplest form, the ear-to-row method of selection is as follows (Fig. 21.2, Scheme I).

1. A number (50-100) of plants are selected on the basis of their superior phenotype. They are allowed to be open-pollinate, and the seeds from individual plants are harvested separately.
2. 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.
3. Several phenotypically superior plants are selected from the superior progenies. There is no control on pollination; the plants are permitted to open-pollinate.
4. Small progeny rows, 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.

21.5.1.1. Modification of Ear-to-Row Method. In order to overcome the defect described above, the following modification may be used (Fig. 21.2, Scheme II).

1. First Year. Several plants are selected on the basis of phenotype (as in item 1 above). Open-pollinated seed of the selected plants is harvested separately.

2. 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.

3. Third Year. The remaining seed from those plants that produced the 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 in U.S.A. and was responsible for the development of several varieties. In this method, plants from superior progenies 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.

21.5.1.2. 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.

1. Seeds for progeny testing are obtained by selfing the selected plants and not from open-pollination. 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.***
2. 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*** (included in the ***half-sib family selection***) and ***reciprocal recurrent selection.***

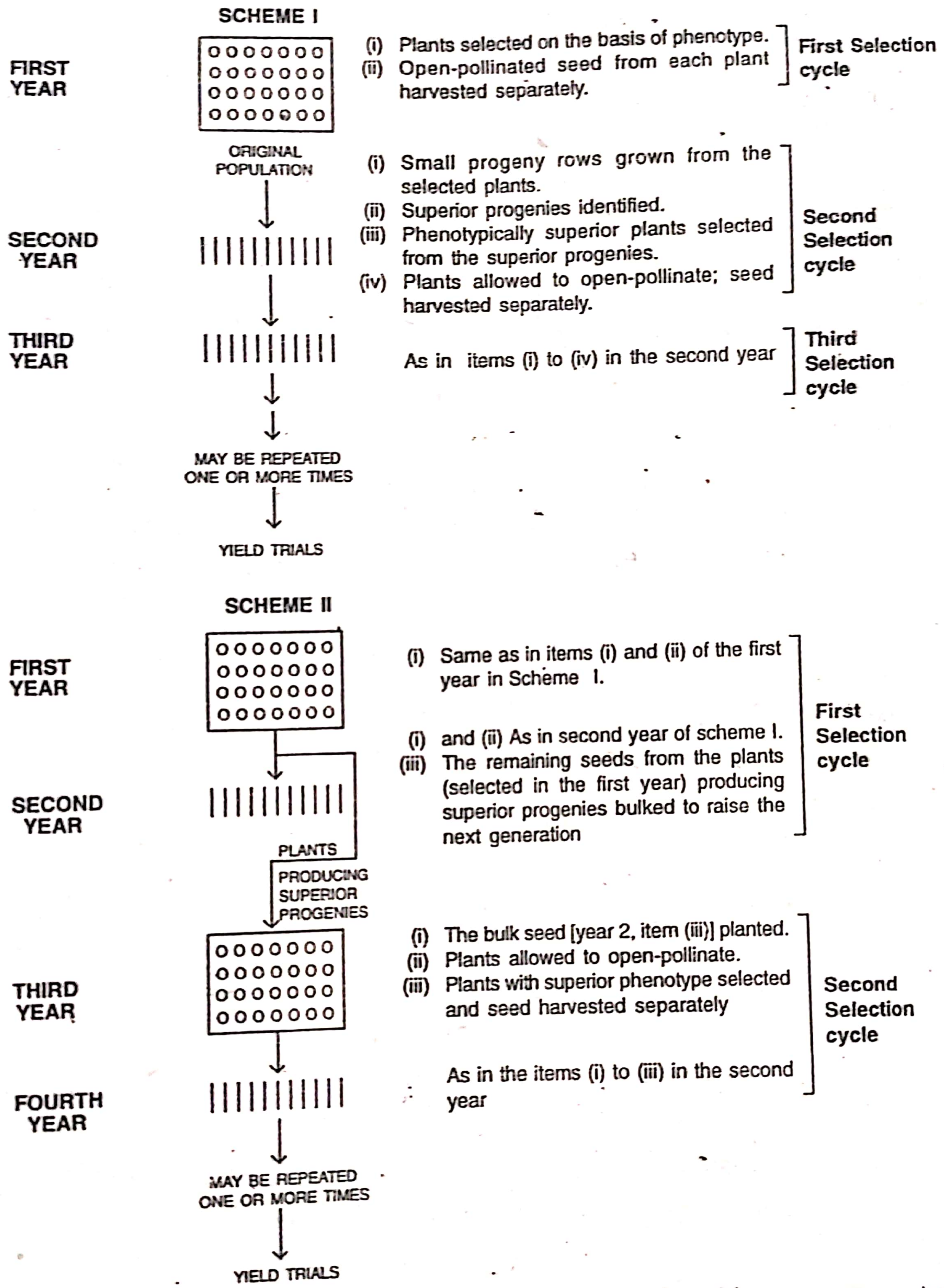

Fig. 21.2. Ear-to-row method of progeny selection as applied to maize. These schemes are termed as recurrent selection by many plant breeders who apply the term to any selection scheme, which has two or more selection cycles.

3. The progeny test consists of a replicated yield trial in place of a single row. In this method, environmental effects can be separated and the actual value of each progeny

can be more accurately estimated. This modification was proposed by Lonnquist in 1964, and is by far the most successful method of progeny selection. In this case, progenies from the selected plants are planted in a replicated yield trial as well as in a crossing block (recombination or seed production plot). The progenies in the crossing block are detasselled; they 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. 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.***

4. 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.***

21.5.1.3. Merits of Progeny Selection. The progeny selection schemes, except those for recurrent selection, have the following advantages.

1. In progeny selection, the selection is based on progeny test and not on the phenotypes of individual plants. The progeny test is a far more accurate reflection of the genotype than is phenotype. Thus progeny selection is far more efficient than mass selection in the identification of superior genotypes. This is a powerful tool for increasing the yielding ability of open-pollinated varieties of maize; the yielding ability increased at the rate of 3-8 per cent per selection cycle in different experiments.
2. Inbreeding may be avoided if care is taken to select a sufficiently large number of plant progenies and if the selected progenies are not closely related.
3. The selection scheme is still relatively simple and easy. But some of the modifications are more complicated and tedious.

21.5.1.4. Demerits of Progeny Selection. The progeny selection schemes, other than recurrent selection, suffer from the following defects.

1. In most progeny selection schemes, there is no control on pollination and plants are allowed to open-pollinate. Thus the selection is based on the maternal parent only. This reduces the efficiency of selection.
2. Many of the progeny selection schemes are complicated and involve considerable work.
3. The selection cycle is usually of two years, *i.e.*, the complete selection process takes two years. Thus the time requirement for selection is twice as much as that in the case of mass selection.

21.6. APPLICATIONS OF MASS AND PROGENY SELECTIONS

Mass selection has been extensively used for the improvement of cross-pollinated crops. Even in the case of maize, where it was almost completely replaced by heterosis breeding, there is a renewed interest in population improvement. Heterosis breeding, as would be seen later, is expensive, time and labour consuming, complicated and requires strict pollination control. As a result, in a vast majority of cross-pollinated crops heterosis breeding is not likely to become economically feasible. In such cases, 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 purity of the varieties of cross-pollinated crops; in some crops, progeny selection is used for the same purpose. The population improvement schemes have been and are being used for the development of new improved open-pollinated varieties of many cross-pollinated crops.

21.7. ACHIEVEMENTS THROUGH MASS AND PROGENY SELECTIONS

Mass and progeny selections have been extensively used for the improvement of cross-pollinated crops. The early varieties of bajra were developed through mass selection; some of the examples are, Babapuri, Jamnagar Giant, AF3, S530 and Pusa Moti; all these varieties were isolated from African introductions. Pusa Moti (developed at IARI, New Delhi) had a wide adaptability and was a popularly grown variety. Mass selection improved the yielding ability of toria (*B. campestris* var. *toria*) by 30 per cent and oil content by 56 per cent; a further increase of 16 per cent in yield was obtained by using mass-pedigree method. Many early, erect to semierect types have been developed in rai (*B. juncea, e.g.*, Type 11, L16), toria (*e.g.*, Abohar), yellow sarson (*B. campestris* var. *yellow sarson, e.g.*, T42, T16); and brown sarson (*B. campestris* var. *brown sarson, e.g.*, 17 dwarf, 17 medium, DS1 and DS2). Selections DS1 and DS2 gave 251 and 286 per cent more yield than the local variety, were earlier by 5-10 days and had larger seeds; they can be planted as late as the first week of December.

Varieties have been developed through mass selection in maize (*e.g.*, T41, T19, Jaunpuri, etc.), cotton [*e.g.*, C402, C520, C1281 and K12 from desi cotton (*G. arboreum*), and 100F, 216F and A19 from American cotton (*G. hirsutum*)], castor (*R. communis, e.g.*, S20, B1 and B4) and in many other crops. A large proportion of the present area under maize is planted to open-pollinated varieties, which are the products of mass selection. For example, Jaunpuri maize is very popular in areas around Jaunpur and is a successful open-pollinated variety. These examples are merely a small sample of the vast range of achievements through mass selection.

21.8. RECURRENT SELECTION

The idea of recurrent selection was first suggested by Hayes and Garber in 1919 and independently by East and Jones in 1920. However, cohesive breeding schemes of recurrent selection were developed during 1940s, particularly after 1945 when Hull suggested that recurrent selection may be useful in improving specific combining ability. *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 isolating an outstanding 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 favourable genes and genotypes in the base population, using a breeding scheme that would keep inbreeding to a minimum.

The recurrent selection schemes 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. The recurrent selection schemes are of the following four different types, 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).

21.8.1. Simple Recurrent Selection

In ***simple recurrent selection,*** (1) a number of plants with desirable phenotype are selected and self-pollinated. (2) In the second year, separate progeny rows are grown from selfed seeds of the selected plants. (3) The progenies are intercrossed in all possible combinations by hand, and equal amount of seed 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 (Fig. 21.3).

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 seeds 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 (Fig. 21.3) is very similar to the Scheme I of progeny selection (Fig. 21.2). However, it differs from the Scheme I in 3 important ways: (1) the selected plants are self-pollinated as compared to open-pollination in Scheme I, (2) the progenies are intercrossed in all possible combinations 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,

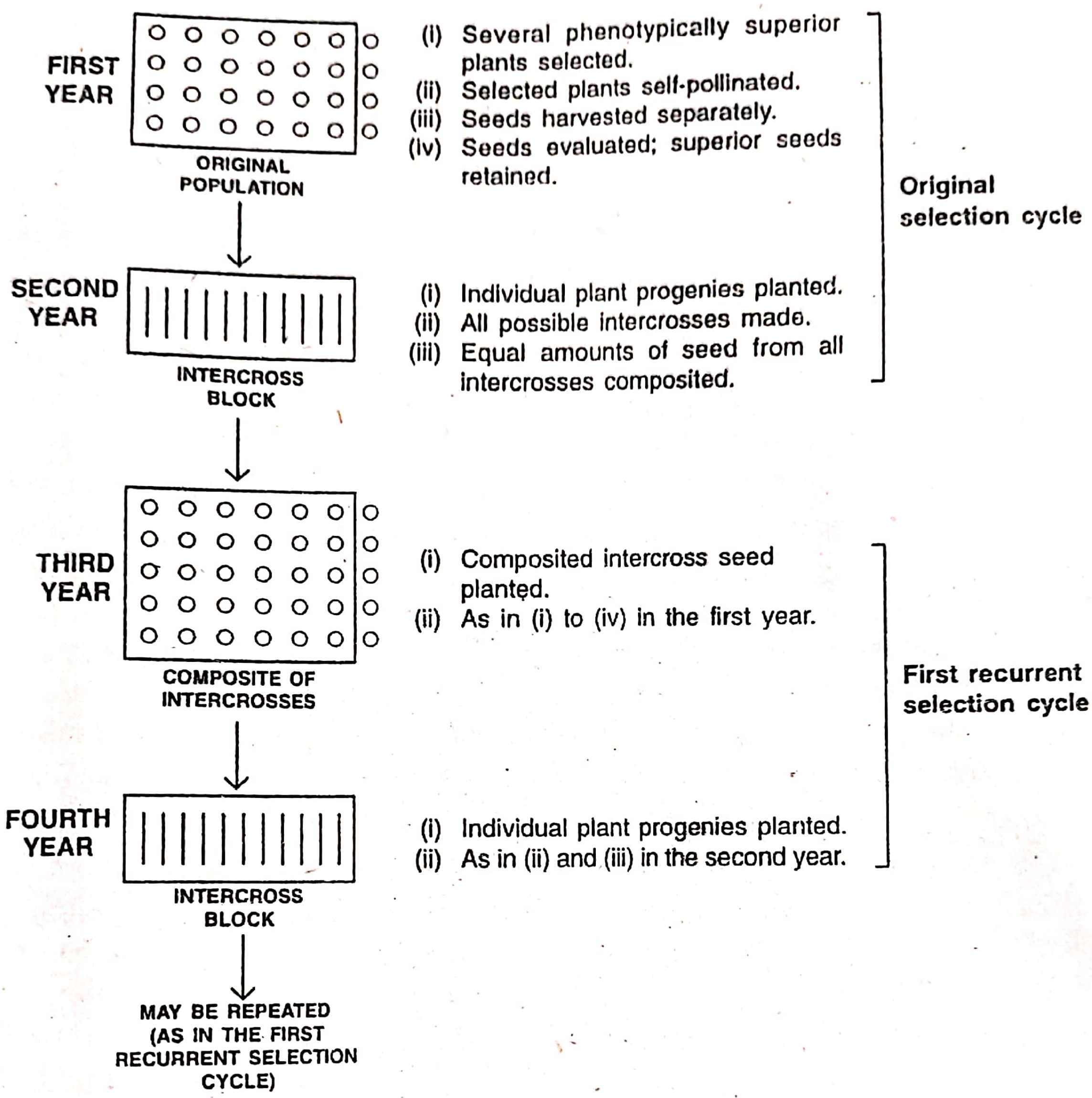

Fig. 21.3. Simple recurrent selection when the characters under selection can be easily evaluated on the basis of phenotype of the selected plants or form the selfed seed obtained from them.

e.g., yield. A portion of the self-pollinated seed from the selected plants is used to plant 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 (Fig. 21.2); the differences between the two are the same as those noted 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 minimised in one of the following two ways: (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 reselection. 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.

21.8.2. Recurrent Selection for General Combining Ability (RSGCA)

In case of recurrent selection for general combining ability, the progeny for progeny testing are obtained by crossing the selected plants to a tester strain with a broad genetic base. A ***tester*** strain is the common parent mated to a number of lines, strains or plants; such a set of crosses is used for the estimation of 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.*, an open-pollinated variety, a synthetic variety or the segregating generations of a double or a multiple cross. Since the gametes from such testers would be variable, the differences between plant × tester progenies would be primarily due to the general combining ability (GCA) of the plants (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 × tester progenies would have superior GCA.

RSGCA is a direct outgrowth of early testing suggested by Jenkins in 1935. ***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 for developing synthetic varieties from short-term inbreds; this scheme is essentially RSGCA. The various steps involved in RSGCA are schematically represented in Fig. 21.4, and are briefly outlined below.

1. First Year. A number of phenotypically outstanding plants are selected from the source population. The source population may be an open-pollinated variety, a synthetic or an advanced generation of a hybrid. Each selected plant is selfed as well as crossed (as male) to a number of randomly selected plants from a tester with broad genetic base. The selfed seeds are harvested separately and saved for planting in the third year. The test-cross progeny (plant × tester progeny) from each selected plant is harvested separately and used for a replicated yield trial in the second year.

2. Second Year. A replicated yield trial is conducted using the plant × tester progenies. The superior progenies are identified.

3 Third Year. Selfed seeds (from the first year) from those plants that produced superior test-cross progenies (identified 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.***

4. Fourth Year. The seed obtained from bulking of all the intercrosses is planted as the source population for the first cycle of recurrent selection. Several plants are selected on the basis of their phenotype; each of them is selfed as well as crossed (as male) to a number of random plants from the tester with wide genetic base.

5. Fifth Year. Operations of the second year are repeated.

6. Sixth Year. Operations of the third year are repeated. This completes the ***first recurrent selection cycle.***

7. 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.

Experimental evidence shows that *RSGCA is effective in changing GCA in the direction of selection. In addition, it is also effective in increasing the yielding ability of the population obtained at the end of selection cycle.* 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 (Fig. 21.4). Obviously, *this population is identical with a synthetic variety and is often referred to as such.* The yielding ability of a synthetic variety developed through recurrent selection may be further improved through additional cycles of selection. Generally, there is some decrease in the variability of the selected population, most likely due to inbreeding. This loss in variability could be prevented if care is taken to avoid excessive inbreeding (see, simple recurrent selection). However, in the case of characters governed by a few major genes, it may be expected that the genes would be close to fixation after a few cycles of selection leading to a decrease in the variability for such characters.

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.

21.8.3. Recurrent Selection for Specific Combining Ability (RSSCA)

Recurrent selection for specific combining ability was first proposed by Hull in 1945. The objective of RSSCA is to isolate from a population such lines that will combine well with a given inbred. It is assumed that a large part of heterosis is the result of nonadditive 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 inbred, 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 GCA, except that in this case 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 to be employed as the tester in an RSSCA programme. The RSSCA selection scheme is briefly outlined below (Fig. 21.4); while referring to the Fig. 21.4, the tester should be read as an outstanding inbred.

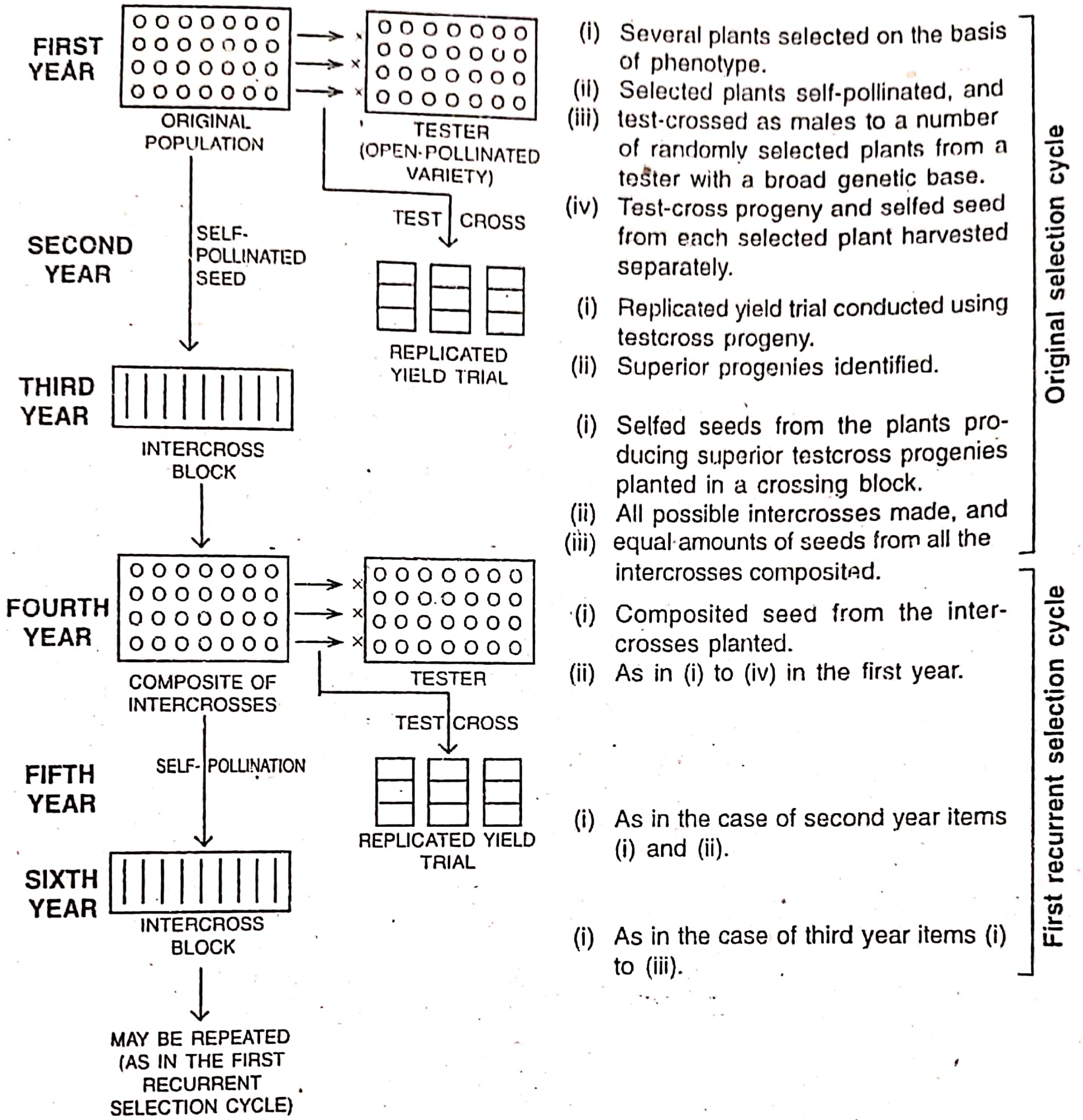

Fig. 21.4. Recurrent selection for general combining ability. In the case of recurrent selection for specific combining ability, an inbred is used as a tester in the place of an open-pollinated variety; the rest of the scehme remains the same.

1. 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).

2. Second Year. A replicated yield trial is planted using the testcross progeny. Outstanding progenies are identified.

3. Third Year. Selfed seed 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 amounts of seed from all the intercrosses are composited. This completes the ***original selection cycle.***

4. Fourth Year. The composited intercross seed is planted and the operations of the first year are repeated.

5. Fifth Year. Operations of the second year are repeated.

6. 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).

21.8.4. Reciprocal Recurrent Selection (RRS)

Reciprocal recurrent selection was proposed by Comstock, Robinson and Harvey in 1949. 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 testers 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 pupulation 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 de crossed with each other to produce the commercial variety, and the plants in each of the two source populations are selected for their ability to combine well with the gene combinations present in the other population, that is, for SCA with each other. A generalised scheme for RRS is outlined below (Fig. 21.5).

1. First Year. Several plants are selected from the populations 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 selfed; 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 (Fig. 21.5).

2. 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 plants 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.

3. Third Year. Selfed seeds 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 amounts 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.***

4. 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.

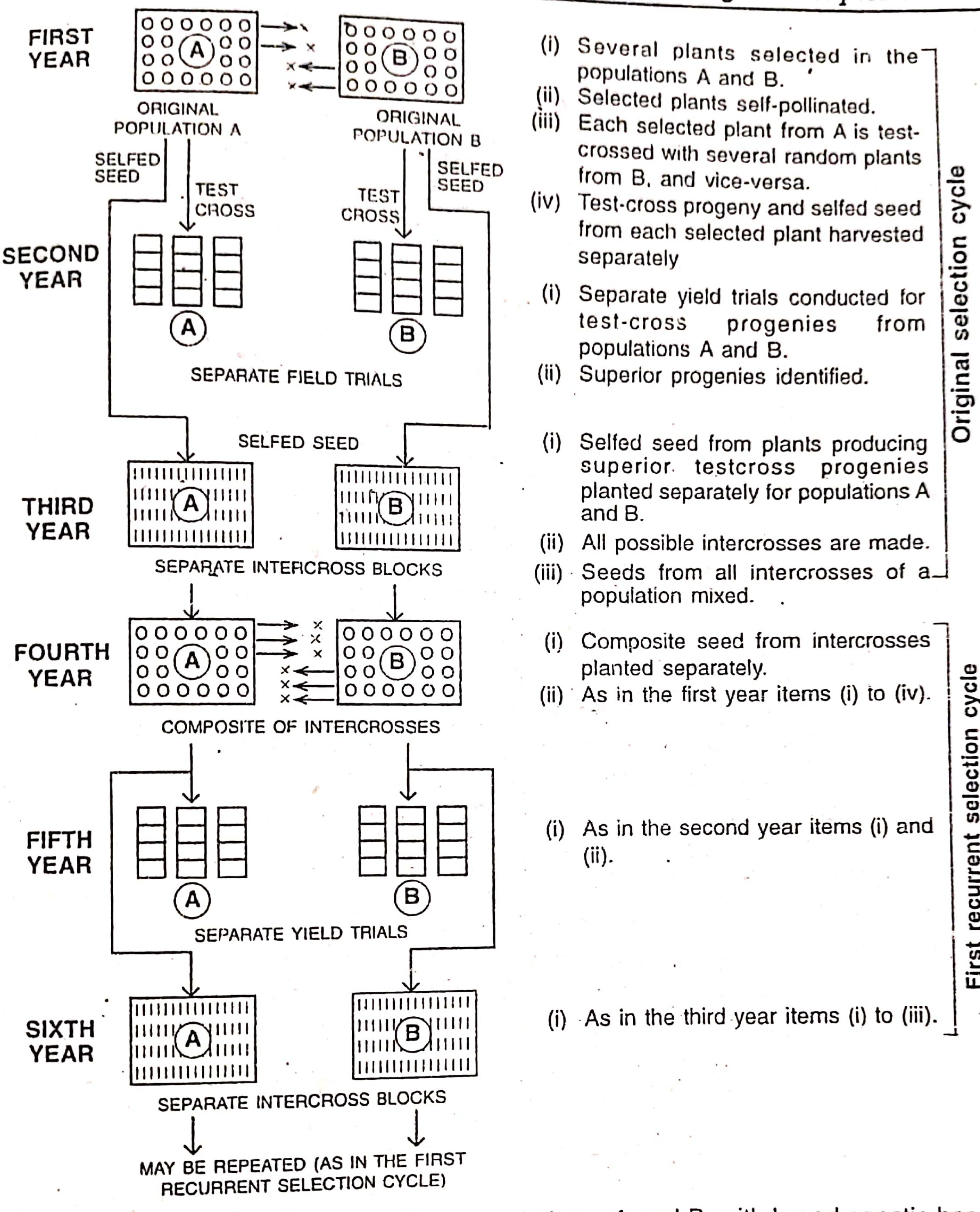

Fig. 21.5. Reciprocal recurrent selection. Two populations, A and B, with broad genetic base serve as testers for each other.

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

6. **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.

1. **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 (see later).

2. **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: $(A_1 \times B_1)$

   Double cross: $(A_1 \times A_2) \times (B_1 \times B_2)$

   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 hybrids produced by crossing inbreds isolated from the selected populations.

21.8.5. Comparison 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.

1. When dominance is incomplete, RRS and RSGCA would be comparable in their effectiveness, and both will be superior to RSSCA.
2. When dominance is complete, the three methods would be equally effective.
3. In case of overdominance, RRS and RSSCA would be equally effective, but both would be more effective than RSGCA.
4. 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.