236 Genetic Basis and Methods of Plant Breeding

- 1. Low proportion of desirable genes in the base material (that is, open-pollinated varieties);
- 2. rapid fixation of genotypes causing hinderances to recombination between favourable genes; and
- 3. limited effectiveness of selection especially for quantitative characters of economic importance.

As a result of this, outstanding hybrid varieties could not be produced. Had there been use of improved inbreds (developed through population improvement) in the hybrid breeding programme, the hybrids would have been much more higher yielder than their contemporary hybrid varieties (Gardner cf. Rao and House, 1972). These ideas ultimately led to the discovery and use of an ingenious breeding system called recurrent selection. The system has several advantages over traditional hybrid breeding system :

- (a) Production of hybrid varieties with substantially higher yield;
- (b) maintaining sufficient amount of genetic variation;
- (c) improving inbred lines to be used in hybrid breeding programme; and
- (d) producing broad-based population varieties as a suitable alternative to hybrid varieties.

Recurrent selection, a method of population improvement (selection and intermating between the selects again and again) is a very wide term and includes several selection procedures. In broadest sense, any cylical scheme of plant selection (mass selection and its variants, simple recurrent selection, recurrent selection for gca or population test cross selection, recurrent selection for sca or inbred test cross selection, reciprocal recurrent selection or reciprocal half sib selection, etc.) aimed at to improve plant populations by increasing the proportion of desirable genes is recurrent selection. Sometimes, therefore, it is difficult to draw a sharp line between mass selection schemes and recurrent selection schemes. Further, there can be several populations with similar variance but with different means (Fig. 19.1). The identification and use of populations with highest mean would certainly facilitates production of best hybrids (Hallauer, 1981). The system, therefore, takes case of the drawbacks associated with traditional hybrid breeding system and can be an effective plant breeding scheme to move off the yield plateau of crops. Furthermore, population improvement methods can be employed in allogams as well as in autogams. The diallel selective mating system of Jensen (1970) described in Chapter 17, is a population improvement method for self-fertilizing crops. Of course, use of population improvement methods in autogams is comparatively more difficult.

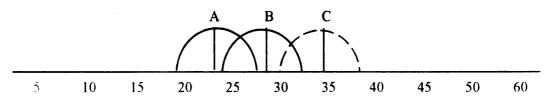


Figure. 19.1. Population with similar variance but with different means

Genetic Basis of Recurrent Selection

The two major forces which are applied during recurrent selection again and again are intermating and selection. The former force continuously generates genetic variability and the latter acts on this variability. If the base material is a random mating population (as is generally the case with openPlants of the source population may be crossed with the tester one generation later, that is, the selected plants of the base population are selfed and the S plants are interplanted with the tester in isolation. Now the cycle would require four crop seasons (selection of promising plants at maturity and selfing, growing progenies of selfed plants and crossing with the tester, evaluation of test crosses in trials for general combining ability and raising selfed seed of promising parent plants in the intercross block). This modified method takes one additional crop season but allows rejection of undesirable S lines at an early stage and makes the handling of the material more easy.

Since recurrent selection for general combining ability is a direct outgrowth of studies of early testing firstly carried out by Jenkins (1935), the method involves following two assumptions :

- (i) Plants of an open-pollinated population show marked differences among them for combining ability; and
- (ii) a plant sample selected on the basis of combining ability test is capable of producing more superior lines than that taken from the same population based on visual selection.

The idea of Jenkins got support from several other investigators (Sprague, 1946, 1952; Lonnquist, 1950; Wellhausen, 1952; and others). All these investigators demonstrated that early testing can help in detecting promising lines which are expected to produce inbred with high combining ability and thus is a good testing procedure particularly when yield is an important consideration. However, the procedure is of limited value where the genes governing the character under consideration have low frequency in the base population. On the other hand, Singleton and Nelson (1945), Richey (1945, 1947), Payne and Hayes (1949) and some other workers expressed different opinion about early testing procedure and considered visual selection as a better procedure (than early testing) for improving combining ability of inbreds in early generations. According to them, rejection of lines in early generations on the basis of top cross tests may result in an uncompensated loss of some promising lines. However, these conflicting arguments regarding the use of early testing could not stop several breeders from adopting this procedure.

Lonnquist (1950, 1951) applied recurrent selection for general combining ability to the openpollinated Krug variety of maize for modifying combining ability and opined that top-cross combining ability can be modified by testing and selection in early generations. However, Mc Gill and Lonnquist (1955) obtained more interesting results regarding the effect of recurrent selection on genetic variability for combining ability in the same maize material. They compared four populations (variety Krug and three second cycle populations derived by recurrent selection) and noted that the genetic variability in Krug variety was significantly larger than in three other populations. Nevertheless, the three derived populations did not show significant differences for genetic variability. If the sufficient care is not taken to check the effect of inbreeding, the genetic variability in derived populations may decrease at a much higher rate than expected during recurrent selection.

Now it is amply clear that recurrent selection for general combining ability can definitely increase the frequency of desirable genes in the population and thus can be considered as an appropriate method for developing synthetic varieties as well as for developing reservoirs of germplasm to extract promising inbreds.

Recurrent selection for specific combining ability: As mentioned earlier, this scheme of recurrent selection was proposed by Hull (1945) and the scheme is also known as inbred test cross selection. As in case of recurrent selection for general combining ability (gca), a cycle here also requires three crop seasons (selection of promising plants from the base population at maturity and selfing as

random mating irrespective of the genotype frequence is in the parent population. Since Syn-2 generation is produced by random mating among all Syn-1 generation genotypes, no further derioration in yield and other characteristics is expected in Syn-3, Syn-4 and so forth.

Maintenance of Synthetics and Composites

Depending upon the floral structure and pollination behaviour of the crop, a synthetic or a composite variety is maintained by open-pollination in isolation or by random mating from hand pollinations among all the genotypes. To maintain the identity of a synthetic variety, the constituent inbreds are maintained and crossed in all possible combinations at regular intervals. However, for the maintenance of a composite variety, a large randomly taken sample of the seed is grown in an isolated area and open-pollination is allowed. A composite variety may be improved by adding some desirable gentotypes.

Natural and/or artificial selection may bring change in the genetic constitution of synthetic variety. This change may be towards positive side (that is, there is improvement in the performance of the synthetic) or towards negative side (that is, reduction in the yielding ability of the synthetic). Incomplete random mating or inbreeding due to smaller sample size or differential selection may also cause change in the performance of a synthetic variety.

Factors Affecting the Performance of Synthetic Varieties

Sewall Wright (1922) suggested a formula to predict the peformance of synthetic varieties. According to him, $1/p^{th}$ of the excess vigour present in the F_1 genration will be lost in the F_2 generation, where p is the number of parental lines comprising the synthetic. The formula may be given as follows :

Syn-2 estimate = Syn-1 mean
$$- \frac{(Syn-1 mean - Syn-0 mean)}{p}$$

Sewall Wright used the terms F₂, F₁, P for Syn-2, Syn-1 and Syn-0, respectively. Here, the estimate of Syn-2 will be determined by three factors, namely, mean of Syn-1, mean of Syn-0 and the number of inbred lines (p) comprising the synthetic. As has been discussed earlier, according to Hardy-Weinberg law, there will be no further deterioration in the vigour in Syn-3, Syn-4 and so on. The experimental proof in favour of the theoretical concept given by Wright (based on Hardy-Weinberg law) comes from the work done by Neal (1935) on single cross hybrids, three-way cross hybrids and double cross hybrids of maize. In Neal's experiment, the average loss of yield in F₂ generation for single cross, three-way cross and double cross hybrids (involoving 2, 3 and 4 inbreds in each cross, respectively) was 50 per cent, 33.3 per cent and 25 per cent, respectively, that is, 1/pth of the excess yield of the F₁. Furthermore, there was no significant difference between the yields of F₂ generation and F₃ generation in case of single and three-way cross hybrids. Sprague and Jenkins (1943) also found similar results regarding the yield levels of F, and F, generations. Therefore, results of Neal's experiment clearly proved that there was a gratifyingly high agreement between Wright's theoretical expectations and the actual experimental results in two respects : (1) The average loss of excess vigour in F₂ generation was 1/pth, and (2) there was no further loss of vigour in F₃ and subsequent generations.

As has been discussed earlier, the three factors which can influence the performance of a synthetic variety are :

(4) Lengthy life cycle : A number of asexually reproduced species are perennials and thus the breeder has to wait for a long time to note complete observations about the breeding material.

(5) Transmission of diseases : Growing plants by vegetative parts (tubers, stem cuttings, etc.) is more risky from the point of view of transmission of diseases. On the other hand, crops reproduced by seeds have less chances of transmission of diseases from one generation to the next.

(6) Germplasm maintenance is difficult and expensive : The maintenance of vegetative parts of plant requires more space and it is not easy to maintain these parts for a long period of time.

Before we discuss the methods and techniques of breeding vegetatively propagated crops, we should know the characteristics of a clone. The important characteristics of a clone are :

- 1. Clones are mostly highly heterozygous and deteriorate drastically on inbreeding.
- All plants of a clone are genotypically identical since a clone is maintained through vegetative propagation and does not face consequences of Mendelian segregation and recombination.
 All plants belonging to a pure line or an inbred are also genotypically identical or nearly identical (in an inbred), but these plants are homozygous or nearly homozygous (inbred).
- 3. Like those of a pure line, the plants belonging to a clone, do not constitute a Mendelian population.
- 4. Selection within a clone (like within pure line or within inbred) is ineffective since there are no genetic differences among the plants of a clone. The phenotypic differences among the plants of a clone are due to environment or genotype × environment interaction or due to both.
- 5. Barring mutations, mechanical mixture and/or sexual reproduction in clones, the clones are immortal. Some viral and/or bacterial diseases may also cause degeneration in the clone.

Methods of Breeding

As in sexually reproduced crops, the same three conventional breeding methods-introduction, selection and hybridization- are used to improve vegetatively propagated crops. However, the handling of breeding material in these crops is different from that practiced in sexually reproduced crops. The main cause of this difference is that the promising material can be selected and maintained at any stage of the breeding programme since there is no fear of loosing genetic integrity of the selected material in this group of plants. Nevertheless, in addition to the conventional breeding methods, some biotechnological techniques like haploid breeding (development of monoploids in *Solanum phureja* and protoplast fusion and development of dihaploids in *S. tuberosum*) and mutation breeding are being used to improve these crops.

Among the three conventional breeding methods, introduction and selection take advantage of the already existing variability, whereas hybridization creates new variability. Therefore, the main steps of the breeding programme will be :

- (1) Indigenous and exotic collection of germplasm from different sources.
- (2) Selection of promising clones from cultivated and wild clones.
- (3) Hybridization among the clones to obtain new gene combinations.
- (4) Selection of promising clones from the breeding material obtained after hybridization.

As has been discussed earlier, promising clone can be selected at any stage of the breeding programme and new variety can be evolved.