GENETIC MALE STERILITY IN WHEAT BREEDING

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(Accepted : 9-ii-1967)

The breeding procedures in a particular crop are determined by its pollination system. By using genetic tools, plant breeders have learned to alter a pollination system to exploit new methods of crop improvement. In several cross-pollinated crops, the production of hybrid seed on a commercial scale was made possible only through the use of cytoplasmic male sterility. The manipulation of genes to secure genetic emasculation and facilitate outcrossing has also attracted the attention of plant breeders working with self-pollinated crops. The possibility of large scale cross-pollination in predominantly self-fertilized crops, opens up new avenues of progress and offers unlimited opportunites for recombination and population improvement. In barley, genic male sterility has been used rather extensively by Suneson and co-workers (Suneson, 1951; Suneson and Wiebe, 1962; Qualset and Suneson, 1966) for the development of synthetic barley populations. These populations have provided valuable material for variety selection as well as fundamental genetic studies.

After Pugsley and Oram (1959) reported genic male sterility in wheat, Suneson (1962) suggested that it should be utilized to facilitate crossing. However, the genetics of this male sterility was not clearly understood. Later Suneson *et al.* (1963) developed a wheat composite cross based on this male sterility. Another source of male sterility in wheat has recently been discovered (Athwal *et al.*, unpublished) wherein the character appears to be dependent on the additive effect of three recessive genes and is influenced by minor genes and environmental conditions. This male sterile line presently is being multiplied in a pure breeding form because it gives a small percentage of seed setting (ranging from 0 to 5 per cent.) under field conditions. Simultaneously, male sterility genes are being transferred through backcrossing to some of the standard varieties in order to maintain them in a heterozygous form. The purpose of this paper is to suggest some methods for the utilization of genetic male sterility in wheat breeding.

As in other self-pollinated crops, wheat breeding has been mainly carried out by selection of apparently homozygous strains following hybridisation between different genotypes. This method utilizes primarily the additive gene effects. The importance of maintaining diverse genetic collections and exploiting

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them in plant breeding work has been fully realized only in recent years. With the availability of a great diversity of genetic material, there remains a large potential yet unrealized before reaching the maximum limits of productivity. The ease and rapidity with which desirable genes from various sources can be brought together will, to a large extent, determine the rate of progress. We recognize that the extensive inter-mating of F_1 hybrids and early generation segregates of many diverse crosses, which facilitated gene recombination, has contributed greatly to the success of the Mexican wheat programme. The use of widely different exotic germ plasm such as the dwarf Norin wheats in crossing programmes led initially to disappointing results, but continued genetic recombination ultimately demonstrated its utility. A rapid approach to homozygosity under self-fertilization is a barrier to progress. Genetic male sterility offers a mechanism for more efficient utilization of additive genetic variance by establishing germ plasm complexes simulating a random mating population. Selection in such populations of corn has shown continuous improvement in yield level (Gardner, 1961; Johnson, 1963) and oil and protein content (Woodworth, Leng and Jugenheimer, 1952).

More recently, the discovery of cytoplasmic male sterility and fertility restoring genes in wheat has opened up possibilities of developing hybrids which will permit the utilization of both additive and non-additive components of genetic variance. This is the first time that a major attempt is being made to commercially exploit hybrid vigour in a self-pollinated crop. The wheat plant has evolved naturally as an inbreeder over a long period of time and is basically not adapted to cross-pollination although self sterile lines may show a considerable amount of outcrossing. Sub-normal seed setting on male sterile seed parents and incomplete fertility restoration in the F_1 are probably the most serious handicaps to the development of hybrid wheat. Both these problems have little significance in a cross-pollinated crop. Recurrent selection in a suitably constituted random mating population should lead to considerable progress in modifying the floral characters which hinder cross-pollination. Although hybrid wheat may be released for cultivation long before much can be done to improve the capacity of the wheat plant to outcross, its floral structure will continue to be an important factor in determining the economics and ultimate success of hybrid wheat.

There is a need for more basic research in support of hybrid wheat programmes. Hybrids have been found to excel the superior inbred parent by an appreciable margin. On evolutionary grounds there is some doubt regarding the relative magnitude of the non-additive portion of variance in self-pollinated crops. Nevertheless, it is difficult to isolate a pure breeding strain which will equal a hybrid with respect to a polygenic character such as yield. Hybrid wheat will give more flexibility to breeding programmes. The shorter time required to incorporate diverse genes for disease resistance in a hybrid will provide a special advantage in the battle against a continually changing pathogen. Hybrid wheat offers the easiest method of combining two different genes (in a heterozygous form), each capable of giving resistance to prevalent races and thus providing double protection against variation in the disease organism.

Some techniques which will utilize genetic male sterility to accelerate the exploitation of existing variability through the development of improved cultures and hybrids are outlined.

Broad based populations for variety improvement.—Essentially, this is the same technique as utilized by Suneson for the improvement of synthetic barley populations through natural selection. It is suggested, however, that artificial selection may be exercised in a germ plasm pool after linkage equilibrium is restored by three or four generations of random mating. This will largely resemble the procedures adopted by corn breeders and animal breeders in population improvement.

A broad based germ plasm pool can be developed by using a collection of varieties and advanced generation lines with a wide range of genetic diversity as the pollen parents. The composition of the material to be used as the pollen source should be governed by the breeder's objectives. For example, if the objective is to develop a variety responsive to heavy doses of fertilizers, the pollen source should have a high frequency of dwarfing and disease resistance genes besides genes for general agronomic desirability. Any information available regarding the general combining ability of varieties would be helpful. The bulked seed of this material may be sown in rows alternating those of the genetic sterile to facilitate cross-pollination. Adjustments in sowing time and agronomic practices will ensure the availability of pollen representing all genotypes for fertilization of the male sterile florets. The next generation would be raised from the seed produced by male sterile lines on outcrossing. Thereafter, random mating conditions or a high degree of cross-pollination can be imposed by harvesting only the seed from highly sterile segregates which are easily identified after flowering. The frequency of the genes contributed by the genetic sterile parent could be reduced, if necessary, by backcrossing sterile heads in the first segregating generation with the pollen source. After several generations of random mating, selection may be practised for such highly heritable characters as disease resistance and lodging resistance on a single plant basis and for less heritable characters like yield on the basis of progeny tests. One or more cycles of random mating and selection can be initiated by reconstituting an upgraded population. The material can be grown at different locations to increase the frequency of genes for adaptation. Improvement in populations will not only increase their value for the isolation of cultures (uniform or heterogenous with high buffering capacity) for direct cultivation, but will also enhance their usefulness as potential parents of hybrids. This is a long range breeding approach to supplement and not to substitute the conventional breeding methods.

Development of populations for a hybrid breeding programme.—Previous breeding work has accumulated a large number of improved wheat varieties, many of which are being converted to cytoplasmic male steriles and fertility restorers by workers in different countries. The combining ability studies before undertaking such conversion are time consuming and laborious. Therefore, the selection of varieties for this purpose has been either arbitrary or based on limited information. It is now generally recognized that conversion to male steriles and fertility restorers is not as easy as it was once presumed. Some lines are easy to sterilize. There are others which can be converted to restorers with greater ease. In order to secure genotypes with the full complement of genes influencing these characters, it is necessary to exercise selection in backcross generations. Inter-mating of different individuals in a segregating population should be helpful in developing efficient restorers. As a long range project to support a hybrid wheat programme, it is suggested that two random mating populations should be established; one designated as AB for extracting cytoplasmic male sterile lines and their maintainers, and the others as AR for extracting pollinators. A schematic representation for the development of these populations is given in Fig. 1.

Population AB can be constructed by growing, in isolation, bulk seed of available cytoplasmic male steriles, genetic sterile and a pollen source, the three kinds of material to be accomodated in separate rows. A collection of selected varieties (non-restorer) could constitute the pollen source. If the genetic sterile has a high frequency of undesirable genes, it may be backcrossed with the pollen source before initiating the population development programme. The succeeding generations should be raised by sowing as separate rows, the seed harvested from CMS (cytoplasmic male sterile) and GS (genetic male sterile); the former will continue to breed pure for sterility and the latter will segregate after one generation. GS will provide pollen to maintain CMS, and also an opportunity for gene recombination. Random mating conditions can be imposed if in the GS lines, only seed harvested from male sterile plants is carried forward. After a number of generations of random mating, mass selection or recurrent selection can be initiated to improve the population in respect to various characters including its potential to yield completely male sterile lines (cytoplasmic). Population AR can be developed by growing bulk seed of available cytoplasmic male steriles with a broad-based pollen source (non-restorer), in an isolation plot, backcrossing once and then by substituting bulked fertility restorer lines as the pollen source. Cross-fertilization will allow the fertility restoring genes to combine with the latent gene pool present in a sterile state. Thereafter, the pollen source should be withdrawn, and the population may be perpetuated from the seed produced on CMS, which will later segregate for fertility restoration. Random-mating conditions will exist as long as the seed of outcrossed sterile plants is used for the next generation. After several generations of random mating, selection may be practised to improve the population, one of the selection criteria being complete restoration of fertility. Improvement in populations AB and AR can be continued, as long as it responds to selection, with a view to intensify desirable characteristics. The material can be grown at different locations to increase the range of adaptation. These populations would be amenable to a scheme of reciprocal recurrent selection broadly resembling the plan outlined by Gilmore (1964) for self-pollinated crops.

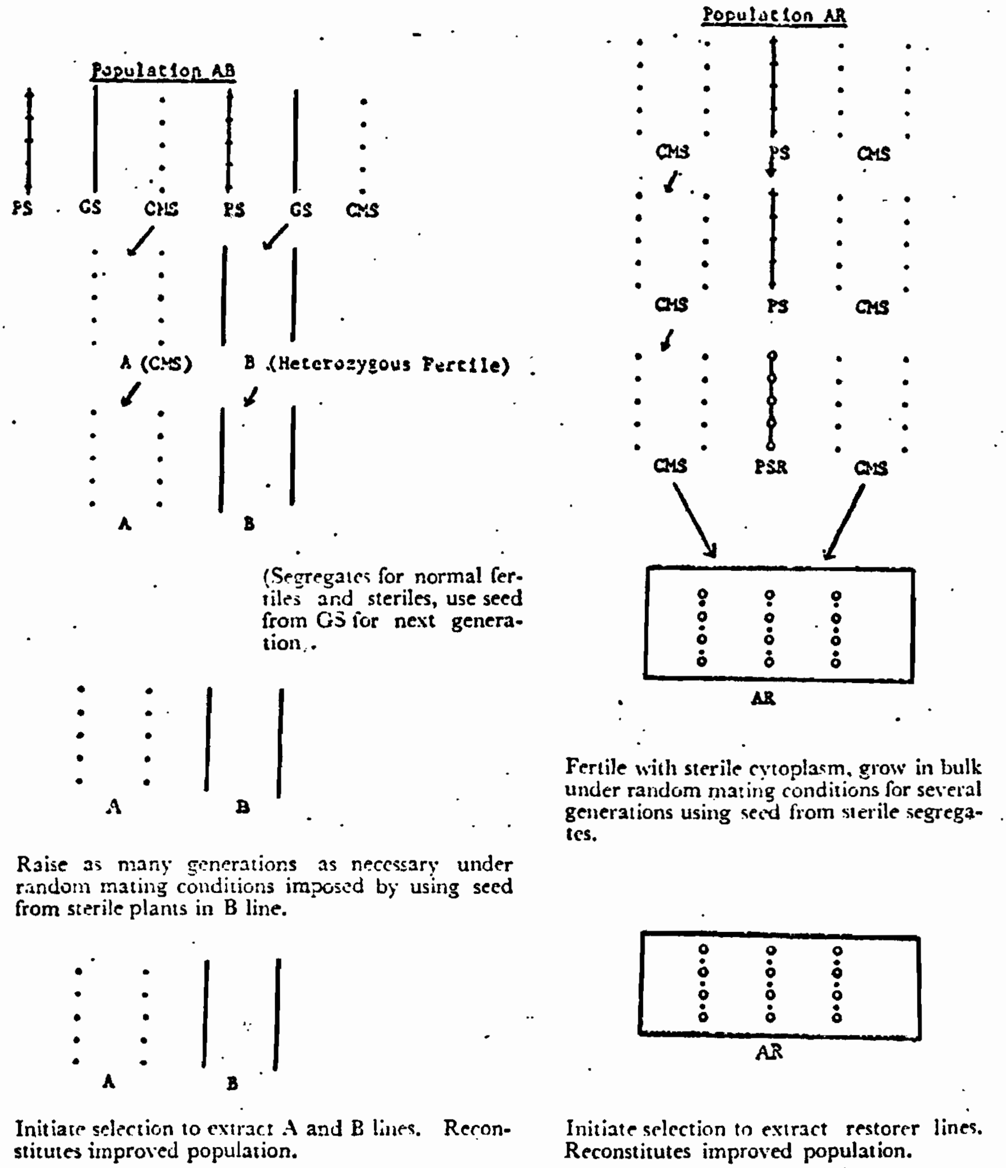

FIG. 1. Diagram showing the establishment of two populations, AB for extracting cytoplasmic male steriles and AR for extracting fertility restorer lines. CMS, GS, PS and PSR refer to cytoplasmic male sterile, genetic male sterile, and nonrestorer and restorer pollen sources respectively. A and B represent a pair of cytoplasmic male sterile and maintainer lines and AR represents genotypes possessing sterile cytoplasm and fertility restoring factors.

Composite populations to improve specific characters.—Recurrent selection in a germ plasm complex undergoing a high rate of genetic recombination through outcrossing provides an excellent opportunity for intensifying or modifying specific characteristics. The genetic gain will be much faster if selection pressure is directed to modify a single trait at a time. Sprague (1966) quoted data from Barley Winter Hardiness Nursery Reports which showed that natural selection under simulated random-mating conditions was highly effective in increasing winter survival. In our work with wheat, it has been possible to increase ear length or number of fertile florets per spikelet by selecting in ordinary segregating populations. There appears to be a vast scope for modifying a character in a desired direction and for developing genetic stocks of considerable breeding value if the unrealized potential of large world collections of wheat is surveyed and suitable germ plasm is selected to constitute random-mating populations based on genetic male sterility. To develop efficient pollinators for use in a hybrid wheat programme, selection can be exercised for plump anther with large amount of pollen and possessing a long filament which will contribute to efficient disposal of pollen. There exists sufficient variation to make such a selection programme fruitful. In order to modify the floral structure of the wheat plant to make it more amenable to cross-pollination, selection pressure can be applied to improve the ability of the floret to open out when the stigma is still receptive. The extent of variability for this character in the wheat collection is not known, but there would be no dearth of the required genes in related plant species or genera. It may be possible to transfer some genes from rye (*Secale cereale* L.) or *Triticale* which would encourage outcrossing. In the same manner, genetic stocks possessing universal resistance to important diseases or high protein content or improved amino-acid balance can be developed. By growing a germ plasm complex constituted by bulking the material possessing resistance to three rusts and raising the populations in different geographical areas, a high frequency of genes capable of giving resistance to different groups of race can be built up.

Summary

The pollination systems of crop plants can be altered by using genetic tools. Any change in the pollination system of a naturally self-fertilized crop which would facilitate outcrossing offers unlimited scope for gene recombination and population improvement. It has been suggested that genetic male sterility should be employed in wheat to create germ plasm composites simulating random mating populations. Selection in such populations will lead to more efficient utilization of additive genetic variance for variety improvement and for the intensification of specific characteristics. A scheme has been outlined for establishing two source populations for the isolation of improved male sterile seed parents and their pollinators in a hybrid breeding programme. These source populations would be amenable to reciprocal recurrent selection aiming to exploit additive as well as non-additive variance in the development of hybrids.

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