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Conventional breeding approaches for enhancing yield potential of rice

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ABSTRACT

By the adoption of semi dwarf rice varieties, rice growing nations have made spectacular advance in rice production during last few decades, enabling to a period of self-sufficiency and surplus. National and International rice improvement programs have not made any significant increase in the genetic yield potential of varieties since the release of IR 8 and have only added values to the semi dwarf high yielding varieties by insulating them with resistance / tolerance to biotic and abiotic stresses. If this trend continues in coming years too then it may not be possible to sustain the self-sufficiency in rice. Therefore, there is a need to raise the genetic ceiling to yield by integrating both conventional and molecular approaches in rice. The following conventional research strategies are suggested to enhance the genetic yield potential of semi dwarf high yielding rice varieties by

- *Exploiting the gene pool concept and use of weedy relatives*
- *Use of disruptive mating and innovative breeding and selection approaches*
- *Mutation breeding to generate mutations at multiple target loci*
- *Male sterile facilitated composite, recurrent selection and population improvement*
- Scope for the development of heterogeneous population

Key words: *Gene pool, recurrent selection, heterogeneous population, stay green trait*

INTRODUCTION

Rice is the major food crop of the world and is the staple food for more than 60 percent of global population. It is the predominant dietary energy source and economically, socially and culturally considered important for consumers in many Asian countries, where 90% of total rice is produced and consumed. In majority of the rice dependent developing economies, rice availability determines food and livelihood security and political stability (Rice Almanac, 2013).

The rice production in India recorded a steady upward trend during the last five decades with a threefold increase in production from 34.5 million tonnes in 1960-61 to 105.24 million tonnes in 2012-13. This has helped in bringing down the quantum of imports and ushering in self sufficiency in food production by mid 1980s.Thus the country has witnessed impressive production and productivity growth trends during eighties, although declined, sustained during nineties due to wide scale adoption of high yielding rice varieties released over past five decades. As a result of enhanced rice production the country made a mark in international trade by becoming the largest exporter of rice in the world earning considerable foreign exchange of about Rs. 43,000 crores during 2012-13 (Shobha Rani et al., 2014).

Being the staple for 65% of the population, at the current level of percapita availability (250gm/day) rice production is required to go up by 40 and 70% - from 105 to145 and 190 million tonnes of milled rice respectively by 2030 and 2050. We would be therefore, requiring to add annually not less than 3.0-3.5 million tonnes of milled rice to sustain the present level of self-sufficiency in rice. It is therefore, a challenging task to achieve this targeted production levels in the next few decades as increase in productivity has to come from the declining and degrading resource base in terms of land, water and other inputs and demand for environmentally sound rice production practices. Practically with no scope for horizontal growth, the projected demand of rice has to be largely through vertical growth. Progressive productivity/production growth of rice being crucial for sustaining self-sufficiency and marching towards food security, planning and prioritizing rationally research and development strategies are important for achieving the near and long term physical availability (Siddiq, 2013; Babu et al., 2015).

It is also a disquietening feature to note that the impressive production and productivity growth rates during eighties has come down during nineties both in India as well as in Asia (Table 1). Further, the experimental evidences have clearly shown that important rice improvement programmes in India as well and at the International Rice Research Institute, have not made any significant increase in the genetic yield potential of varieties released after IR 8 and no perceptible yield improvement has been achieved since 1980 (Virmani et al., 1993; Khush, 1995; Peng et al., 1999). If this trend continues in the coming years too and if we fail to stabilize the yield growth level at least at where we stand today, then it may not be possible to sustain the level of sufficiency the country has achieved in rice. Therefore, there is a need to make concerted research efforts to raise the genetic ceiling to yield only through vertical yield growth.

Plant breeders today argue that, there is hardly any evidence of yield plateau for any crop including rice. Siddiq (1991), has pointed out that continuous growth, no doubt with plateaus at different phases since 1900 suggest that

- A perfect variety has yet not been evolved.
- Still there is an unexploited genetic variability for improving the direct and indirect components of yield through utilization of untapped exotic germplasm.
- There is enough scope to develop and use more efficient breeding and selection techniques for yield improvement in rice.

I. Mating systems

Biparental crosses are widely used in rice varietal improvement programmes to serve the purpose of combining simply inherited traits from two parents. Since the introduction of nitrogen responsive high yielding dwarf varieties the breeding, objectives have become more and more diverse and it was no more possible to combine desired characters to desired norm through biparental matings or in other words the recombination possible from biparental crosses are too restrictive to make rapid improvement in a selfing species like rice.

Table 1. Growth rates (% / year) of rice area, production and yield in India and Asia

Region	Period	Area	Production	Yield
India	70-79	0.87	1.88	1.01
	80-89	0.41	3.55	3.14
	90-99	0.65	2.00	1.34
	2000-2011	0.00	1.72	1.72
Asia	70-79	0.69	2.36	1.67
	80-89	0.19	2.59	2.40
	90-99	0.62	1.70	1.09
	2000-2011	0.51	1.60	1.09

To overcome this genetic limitation, the use of multiple crosses as suggested by Harlan, Martini and Stevens (1940) involving 16-32 parents which are crossed in successive generations until the final hybrid involve all the parents, could be effectively used in rice. Theoretically the multiple crosses provide an opportunity for recombination of genes from many parental strains by intermating F_1s in successive generations. However, it is practically not possible to get enough F_1 seed in later generations of mating cycles to retain all the parental genes in the final hybrid. The second practical limitation was suggested by Mackey (1954) that by using 16-32 parents in a multiple crossing programme will force the inclusion of number of unadapted strains, which are likely to disrupt the good genetic background of varieties that took several years even decades to assemble and therefore suggested modified backcrossing programmes to obtain optimum parental lines and each unadapted parent should be crossed and backcrossed to an adapted variety before its use in a multiple crossing programmes (Fig. 1).

Three way crosses were tried in many selfing species where the third parent is another adaptable germplasm, serves the purpose of increasing the proportion of adaptable germplasm and simultaneously widen the scope for combining desirable genes from another good parent. It has been observed that the populations of three way crosses had larger genetic

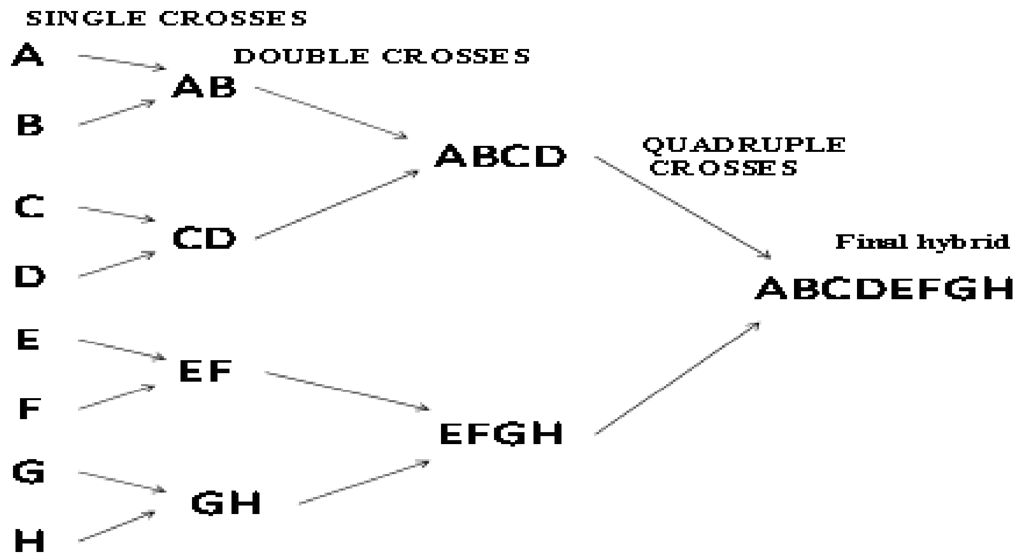

Fig. 1. Multiple crossing programme

variance than biparental crosses and produced more superior lines than two way crosses. Such crosses also provide an element of gamete selection, since the superior performance of test cross F_1 plant reflects the combination of superior gametes from the segregating sinele cross with genotypes of the non-segregating variety as the third parent. As argued by Stadler (1944) the frequency of superior gamete is much higher than the frequency of superior zygote and hence three way crosses provide a more efficient mating system for obtaining lines with better performance (Sharma, 1989). Double crosses involving four different parents were also useful in extending the range of parents and achieve recombination of desirable alleles from diverse parents.

The different mating systems as suggested were limited to a great deal by the requirement of large number of F_1 seeds. As the F_1 generation serves itself as the segregating population similar to F_2 of single crosses and set the limit of possible recombination of genes available in the population. Never the less, these multiple crosses are expected to generate an array of genotypic variability which never existed earlier in any breeding population.

Multiple crossing has hardly been employed in rice breeding programmes. It is interesting to note that out of 427 rice varieties released up to 1992 in India (37 in sixties, 153 in seventies, 205 in eighties and 32 varieties in nineties) only one variety was derived from multi-parents, thirteen from three way crosses and three varieties were double cross progenies. It is not surprising that many rice breeders have not used multiple crossing programmes for varietal improvement in rice because they could get adequate success through careful manipulation of biparental progenies. However, the limited success achieved through various mating schemes employed in rice is primarily ascribed not only to the requirement of large number of F_1 seeds but also relatively small sample size in F_2, where the full range of yield is not realized. Still there is scope to make use of multiple crossing programmes for creation of a wide array of genetic variability and which would facilitate selection of superior individuals for substantial yield improvement in rice. A majority of breeders have restricted their selection to known material and have made intense efforts for local adaptation, as a result certain gene blocks are rapidly fixed along with correlated response which in many cases are adverse in direction. Therefore, it is suggested to choose the parents on the basis of wide genetic base with acceptable level of productivity and high general combining ability before their use in a multiple crossing programme for realization of high and stable yields in rice.

II. Gene pool concept and use of weedy relatives

The gene pool concept for plant breeding was conceived by Harlan and de wet (1971) which divides the total array of genetic variation within the reach of plant breeders, into primary, secondary and tertiary gene pools. Often the primary gene pools include the progenitor of cultivated species that can easily be crossed with cultivated type and produce fertile hybrids with normal segregation.

Frey and his group over a period of 20 years have successfully demonstrated that the ancestral forms Avena sterilis in oat occur in the primary gene pool, has been a valuable source of germplasm for increasing crop productivity. The interspecific oat matings between. A. sativa and A. sterilis showed a great deal of transgressive segregation and Frey (1976) have shown that a considerable amount of yield improvement ranging from 3 to 29 per cent was achieved through such matings, while the agronomic traits similar to the recurrent parent was maintained in BC_3 to BC_5 generations. Further, three elite lines were derived from the second cycle of breeding with A. sterilis, showed a considerable yield improvement of 26 to 31 per cent and were subsequently released to Midwestern USA farmers. The development of elite lines from such matings takes advantage of nuclear genes from A. sterilis and thus adds a quantum increase in yield potential of cultivated oat varieties in USA.

Similarly, results from introgression of the germplasm from H. spontaneum into cultivated barley to increase productivity are equally as exciting as those from oat study (Rodgers, 1982). Promising barley lines with impressive yield advance (29 to 46 %) and with moderate to good levels of agronomic traits were realized in BC_3 to BC_5 generations. In those back cross generations the expected proportion of germplasm from wild species is 6.25 % or less and it is a general phenomenon that both oat and barley can tolerate about the same percentage of wild germplasm for expression of improved productivity.

Nayar (1973) reviewed the genomic relationship among Oryza species and established that both the cultivated species *O. sativa* and *O. glaberrima* and their related wild species such as *O. nivara*, *O. rufipagon, O. breviligulata* and *O. longistaminata* have the same AA genome and they share a common gene pool. These weedy species can be easily crossed with cultivated types and their F_1 hybrids have normal chromosome pairing but show varying levels of sterility.

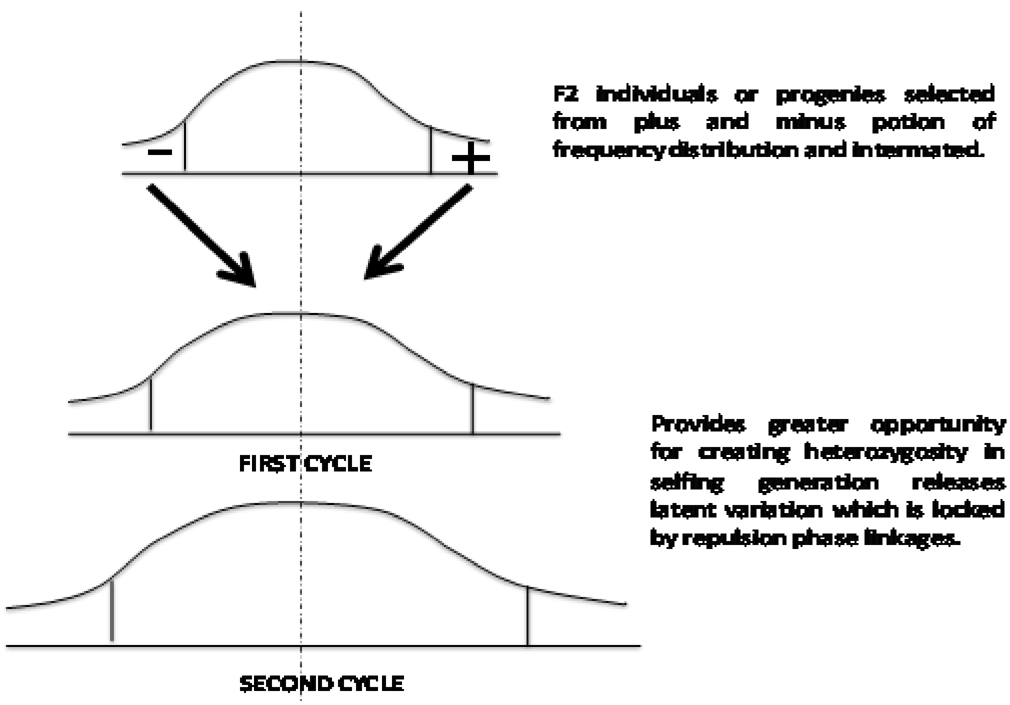

Fig. 2. Disruptive matings in plant breeding

More often the wild species in rice have been used for transferring resistant genes into cultivated type but never been systematically exploited for increasing higher productivity in rice. Therefore, it is suggested to make use of weedy and wild species from the primary gene pool and examine the feasibility of wild germplasm for improving yield potential, like oat and barley, in rice.

III. Disruptive matings in plant breeding

When breeders attempt to make use of unthrifty wild or weedy sources for yield enhancement the chances of success is remote due to the problems of linkage. Linkages drag undesirable alleles into the breeding population as is usually linked to favourable gene and thus discourage breeders from using exotic germplasm sources. There are several instances to demonstrate that repulsion phase of linkage do not express a portion of the potential genetic variation for a trait. To overcome this undesirable genetic limitation Mather (1953, 1955), Thoday (1958, 1960) had suggested the use of disruptive mating in cereals (Fig. 2).

Generally samples of individuals or progenies are selected from plus and minus portions of the frequency distribution and only plus and minus matings are made. Over cycle of such disruptive matings, it is seen that the population mean remain unchanged but the variance and range of the frequency distribution is increased many folds (Blumer, 1976).Theoretically disruptive mating via mating unlike offers greater opportunity for creating heterozygosity in selfing generations and enhance rapid crossing over and releases latent variations which are locked up by repulsion phase of linkages. Although, through such matings the mean remained unchanged but it does not necessarily mean that superior individuals with improved yield potentiality and better agronomic features could not be recovered. The value of disruptive mating for improvement of flowering period, plant height and grain yield in Brassica campestris var. brown sasson has been experimentally verified by Murty et al. (1972) which confirmed the breaking up of repulsion linkages for increasing the genetic flexibility of the population. However, Frey (1984) is of the view that disruptive mating is considered to be an effective plant breeding procedure as more exotic germplasm sources would be used in future plant breeding programmes for improving the direct and indirect components of yield.

IV. Innovative breeding and selection approaches

So far not many rice breeders have utilized novel breeding or selection approaches in the topics as the pedigree selection in biparental progenies having provided them adequate success (Ikehasi and Fujimaki, 1980). However, when the breeding objectives become more and more diverse and the difficulties like complex inheritance, low heritability and linkage of undesirable traits compelled them to make use of more efficient breeding/ selection methodologies to overcome various genetic limitations for rapid progress in crop improvement.

Bulk method of breeding or its modified versions like single seed descent (SSD) method coupled with rapid generation advance (RGA) was successfully employed for rice breeding in Japan and steadily gained popularity among rice breeders (Kikuchi, 1978). Although bulk method of breeding was not found useful in breeding for high yielding dwarf varieties on account of the fact that natural selection operates in eliminating desirable dwarfs which are poor competitors, yet the major objective of this method is to attain homozygosity earlier to pedigree method of selection when it is coupled with RGA. It has been effectively utilized for breeding photosensitive long season varieties (Ikehasi and Nieto, 1977).

Single seed descent (SSD) a modification of original bulk method, is a breeding procedure in which fixation of traits with minimum bias from potential variability is achieved. To prevent any drift in segregating populations, a single seed should be harvested from each F_2 plant to grow F_3 population and that the same procedure be repeated until F_3-F_6. Ikehasi and HilleRislambers (1977) discussed the details of this method in relation to rice breeding and also suggested for an international integrated breeding programme for the development of photoperiod-sensitive rices.

Rapid generation advance (RGA) is not a breeding method but a way of growing bulk populations. Since the major objective of SSD is to attain homozygosity prior to pedigree selection, it becomes essential for rapid cycling of breeding materials that shortens the growth duration of a given population. A large number of plants can be accommodated in limited space and dense spacing because only one or two seeds from each plant are enough to advance the segregating generations. Thus the SSD method is most appropriate for RGA. Success in RGA largely depends on minimum growth duration that can be induced in a specific growth condition. It has been demonstrated that for breeding photoperiod sensitive rice in the tropics, three generations a year can be grown through RGA (Ikehasi and Nieto, 1977; Ikehasi and Hille Ris Lambers, 1979).

Comparison of pedigree, SSD and bulk method of breeding

Casali and Tigehelar (1975) compared pedigree selection (PS), single seed descent method (SSD) and bulk population methods (BP) through computer simulation studies. They found that for characters with high heritability, PS was most effective while SSD was found to be most effective for traits with low to very low heritability and also offered the greatest benefits in situations where simultaneous selection for several traits having different heritability's has to be done.

Knot and Kumar (1975) and Fahim et al. (1998) from two crosses in wheat and rice respectively compared F_6 lines derived through PS and SSD in replicated yield trials and established that the mean yield of PS lines were significantly higher than those of SSD lines. A comparison of 20 % highest yielding lines derived from both the methods indicated that the SSD lines were at least as good as PS lines. Studies by Pawar (1985) clearly indicate that SSD method was found better than bulk method of breeding and PS was superior for grain yield/plant and other yield components than that of BP and SSD populations.

Several workers have compared various breeding methods in predominantly self pollinated crop plants. The published reports by Tee and Qualset (1975), Boerma and Cooper (1975), Haddad and Muehlbauer (1981), Pawar et al. (1986), Nanda (1990), Mishra (1991) and Mishra et al. (1994) reveal conflicting results on the superiority of one method over the other. Although a definite trend of efficiency of different breeding methods is suggested, there are several instances to show that the superiority of any breeding method in retaining the high yielding lines largely depend on the choice of parents in different crosses, interaction between genotype and environment, sample size, genetic drift and changes in gene frequencies due to inbreeding and heritability of traits. As far as the knowledge goes there are very few reports in rice to establish a general trend of relationship and therefore, it is suggested to workout precise experiments to study the efficiency and effectiveness of different selection methods, for realization of high yield in rice.

V. Male sterile facilitated composite

In the pedigree method of breeding the chances of genetic recombinations is too restrictive because the selfing populations rapidly approach homozygosity. Another method for increasing genetic variation is the composite method of breeding which has been extensively applied in barley breeding by Suneson (1956). In this method F_2 of several crosses are bulked into a composite population and subjected to natural selection in diverse environments. The strategy enhances genetic variability which is only confined to two parental strains of each cross, as there is no outcrossing among hybrid plants in the population. But introduction of male sterility into the segregating population help to enhance recombination through natural crossing and Suneson showed that natural selection had caused the bulk population to become higher yielding in later generations. Several composites developed by means of the male sterility factors were investigated by Jain and Suneson (1966) for quantitative genetic changes in variability and productivity. These composites exhibited a very high degree of genetic variability and the increase of genetic variability however not accompany correspondingly increased productivity.

Before using bulk population of breeding as an efficient tool for crop improvement, one must critically analyze the advantages and disadvantages of this method of breeding. Spitters (1979) argue that in bulk propagation, progress made in the later generation may be too slow to be of value to a breeder as the final yield level does not guarantee recovery of high frequency of high yielding lines. However, the bulk population breeding has its own merits under certain conditions. When an economically important trait for instance is controlled by several recessive genes, the chances of recovery of recessive types in later generations are more, which was pointed out as an advantage of SSD approach (Brim, 1966). Also, due to close linkage there is delay in fixation of characters and therefore, selection is advocated in later generation. Ikehasi (1977) has also

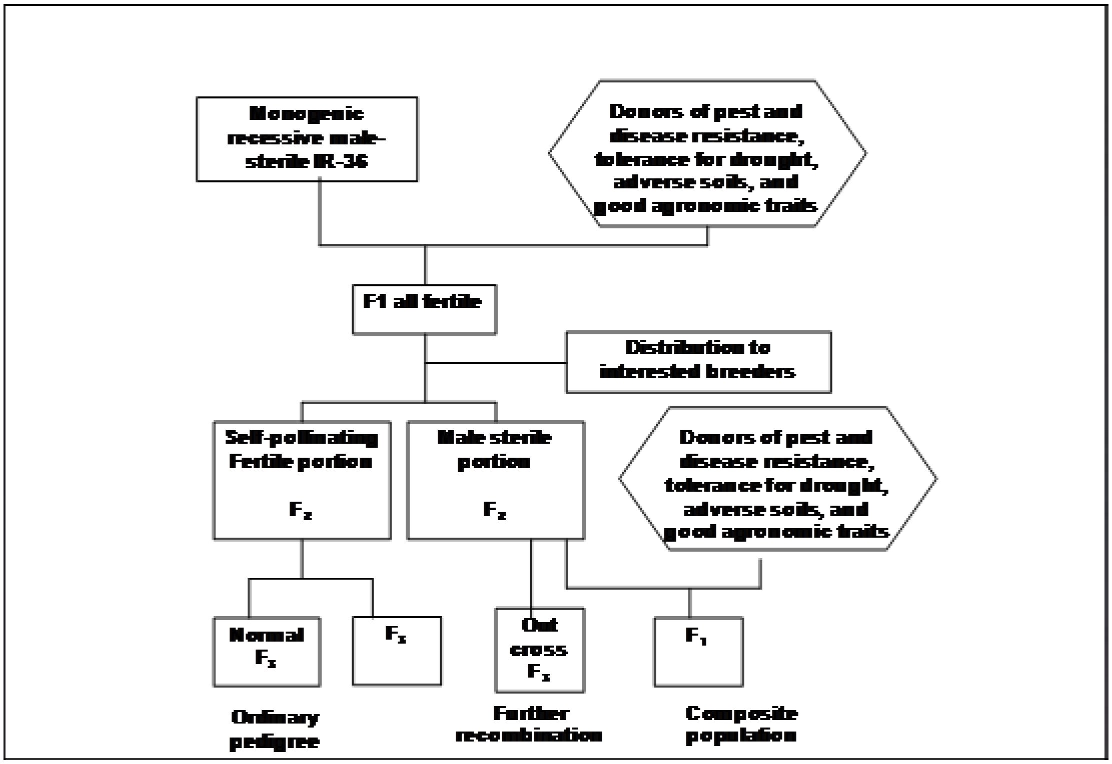

Fig. 3. Monogenic male sterility facilitated composite populations in rice

shown that the proportion of good recombinants from undesirable linkages canbe increased by F_4 and F_5 through additional recombination. Finally, the most important advantage of bulk breeding is to handle large genotypic variation generated from multiple crosses or composite populations and the segregating population which can not be managed through pedigree selection. Further the role of natural selection is most crucial for causing the evolutionary changes in the mean expression of a trait in a bulk population of segregates in a selfing species and can exert strong selection pressure for characters of very high adaptation. Evidences suggest that natural selection would cause either no change or change in a desirable direction. Nevertheless by artificial selection the bulk population may be shifted towards agriculturally desirable types.

The original concept of the bulk population method has been remarkably diversified by SSD, RGA and male sterile-facilitated composites. Ikehasi and Fujimaki (1980) have pointed out that the breeders are now capable of integrating one or more of the bulk method-related means to build the most efficient system for any breeding objectives. It is particularly significant that modifications in bulk population are to handle maximum genetic diversity with least cost and time.

So far male sterility facilitated hybridization has not been employed systematically in rice breeding. Male sterile mutants have been developed from IR 36 at IRRI (Singh and Ikehasi, 1981). They have suggested an integrated method for combining pedigree as well as bulk methods to develop composite population in rice, through male sterile facilitated system, for higher recombination by breaking up parental linkage groups and which may help to form a better base population for the development of best yielding, highly homozygous and homogeneous lines (Fig. 3).

VI. Recurrent selection and population improvement

The plant populations developed from the introgression of exotic germplasm followed by disruptive mating could be subjected to any selection procedures immediately. For short term goals pedigree selection or some modifications would be appropriate while for long-term goals recurrent selection would be the suggested procedure (Frey, 1983,1984).

Recurrent selection is primarily used to promote recombination and to increase the frequency of favorable genes for quantitatively inherited traits in population. It is cyclic and in each cycle two phases of plant breeding *viz.,* selection of a group of genotypes that possess favorable genes and mating among the selected genotypes to obtain genetic recombination. Thus it helps to gradually increase the frequency of favourable genes until there is reasonable likelihood of obtaining the ultimate genotype in a finite sample. It can be applied to the improvement of quantitatively inherited traits in either allogamous or autogamous crop species, irrespective of the type of gene action involved in the determination of the trait. There are many instances to demonstrate that breeders have used this procedure mostly in cross-pollinated crop plants as there is no barrier in intermating favourable genotypes for enhancing genetic recombination among linked alleles in a population of plants.

But the obstacles to genetic recombination among alleles at closely linked loci still remained as a significant barrier to making improvement in self fertilizing species. With selfing heterozygosity which is necessary for effective crossing over and recombination of alleles at closely linked loci decreases very rapidly to an effective level. In order to avoid this genetic limitation Suneson (1945) introduced a male sterility gene into his famous barley composites to promote outcrossing and facilitate random mating without difficulty, for release of variability which is locked by linkage, which helps in the utilization of diverse sources, for practical crop improvement programmes. However, use of male sterility in the mating programmes has a decided selection disadvantage in the population and its frequencies decrease to a very low value within few generations and thus the effectiveness of this mechanism in promoting heterozygosis for increased crossing over would be ephemeral. There is also some evidence that too much crossing over in selfing species can be detrimental to fitness (Frey, 1975). Further if there is no prior selection of desirable types, the benefits of intermating among progenies as advocated by Hanson (1959) would not have any practical advantage over continued selfing. Therefore, particular attention should be paid to intermating in a system of recurrent selection.

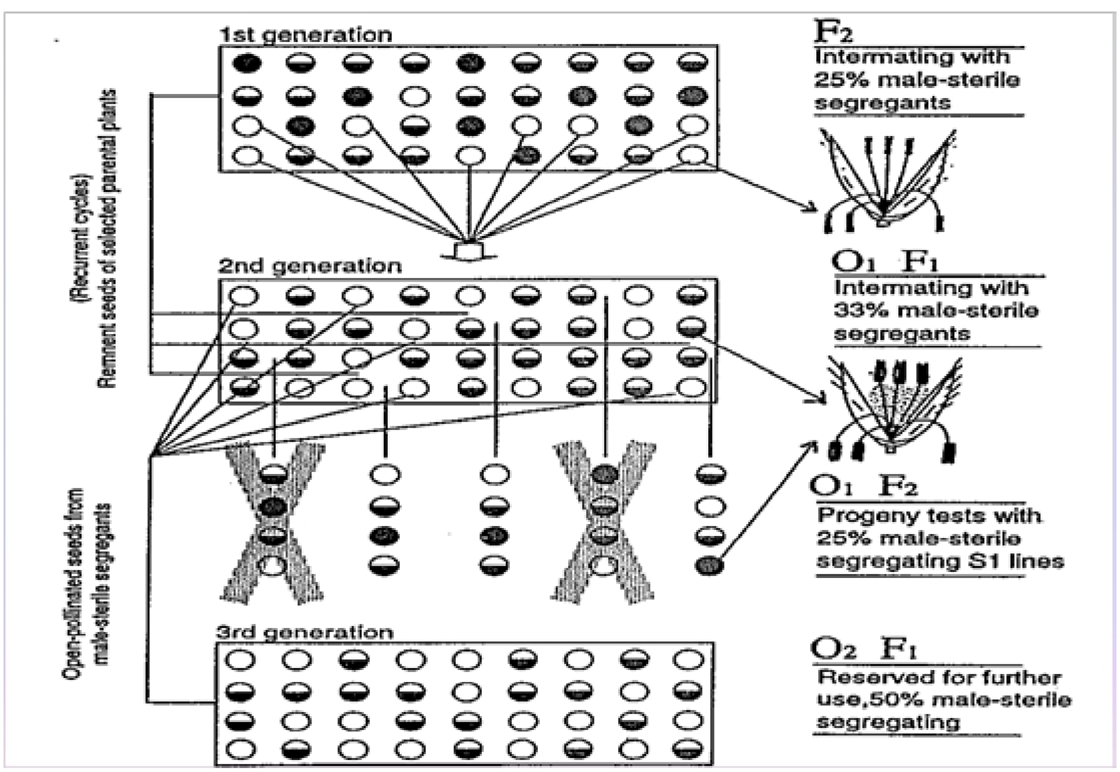

Fig. 4. Male-sterile facilitated recurrent selection for rice breeding

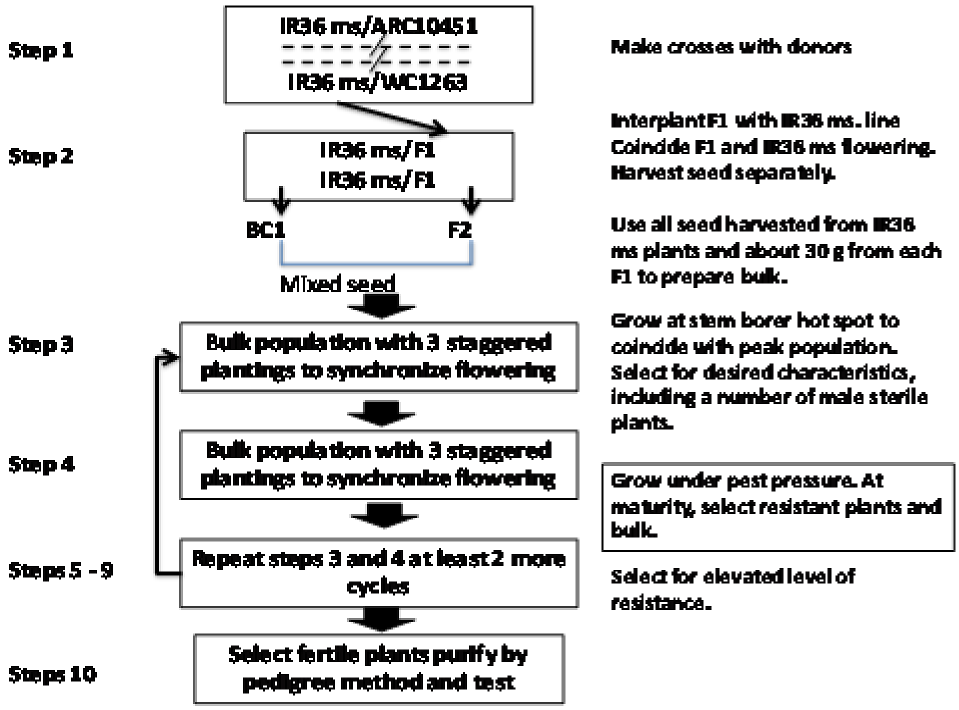

Fig. 5. Male-sterile facilitated recurrent selection to elevate level of Stem Borer resistance

Male sterile facilitated recurrent selection was first suggested by Gilmore (1964) for the improvement of predominantly self-pollinated crop plants. Application of genetic male sterility to recurrent selection was also proposed in breeding of sorghum and soybean (Doggett and Eberhart, 1968; Brim and Stuber, 1973).

Male sterility facilitated recurrent selection schemes were systematically employed in rice breeding after the availability of a male sterile mutant of IR 36 at IRRI (Singh and Ikehasi, 1981). Fujimaki (1978, 1979) initiated programmes to transfer polygenically controlled horizontal resistance to blast and major-gene resistances to BLB into the most popular rice variety 'Nipponbare' in Japan through recurrent selections (Fig. 4). Similarly it was also possible to obtain hybrid population closely resembling the recurrent parent 'Nipponbare' in days to heading, plant stature, grain shape and other morphological traits along with smoothness of rice plants which effectively reduce dust generated in harvesting, threshing and hulling operations through male sterile-facilitated backcrossing in rice.

Chaudhury et al. (1981) suggested a ten step procedure, involving twenty six stemborer tolerant donors, to increase the level of resistance to yellow stemborer through male sterile facilitated recurrent selection in rice (Fig. 5).

Sahai and Chaudhury (1993) also outlined a male sterile facilitated recurrent selection scheme for the development of rainfed lowland varieties in rice (Fig.6).

Although many workers have outlined male sterile facilitated recurrent selections in rice, but an extensive recurrent selection project was initiated in Brazil using the recessive male sterile gene of IR 36 in1984 under the auspices of CIRAD-CA, CIAT, WARDA and IRRI for broadening the genetic base of gene pools in tropical upland japonica, lowland tropical indica, upland and irrigated tropical high altitude and irrigated temperate japonica rices. Several gene pools and populations were developed which have been used as genetic base population for recurrent selection in different Latin American countries like Brazil, Chile and Colombia and in several African countries *viz.,* Ivory coast, Mal, and Madagascar. In 1989, the basic gene pools CAN IRAT-4 and 5 for tropical indica irrigated and tropical japonica upland conditions were made available to the international scientific community. In 1990, at CIAT a hand crossed recurrent selection project began focusing on the development of gene pools and populations targeting blast resistance inr ice (Chatel and

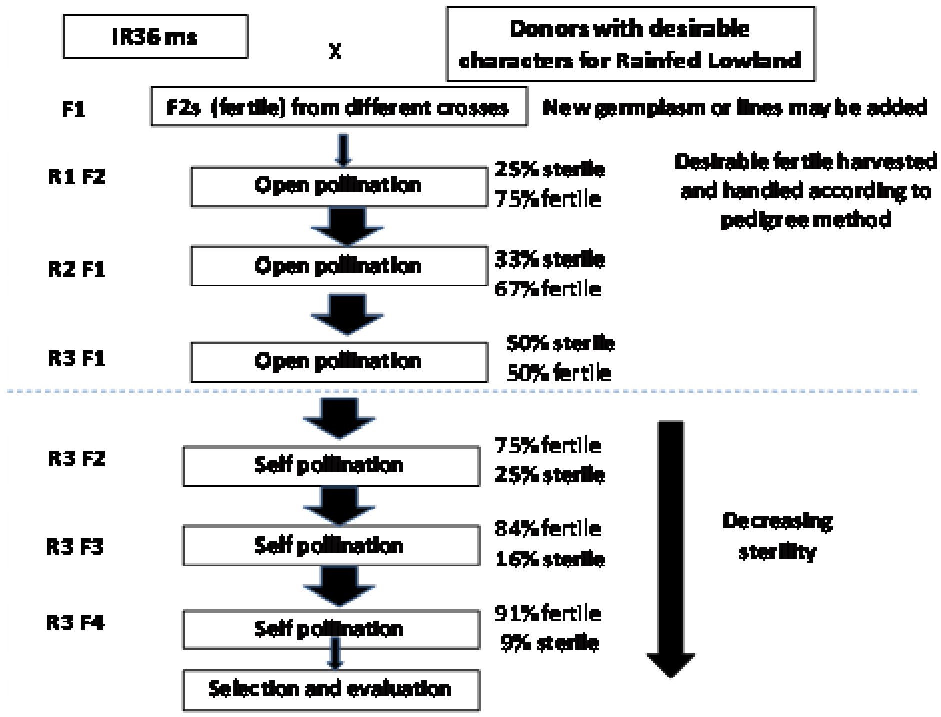

Fig. 6. Male-sterile facilitated recurrent selection in rainfed lowland rice

Guimaraes, 1994).

They have concluded that rice recurrent selection programme has been successful in reaching its maturity. It has derived new gene pools and populations targeting different rice ecosystems and improvement of specific traits like grain quality, resistance to blast, tolerance todrought and yield potential. CIRAD-CA and CNPAF developed the indica and japonica basic gene pools CAN-IRAT 4 and CAN-IRAT-5; CIRAD-CA and IRRI developed indica-japonica CPI 22L and indica CP 126 gene pools and CIAT developed the indica-japonica gene pool GC 91 by hand crossing.

Presently breeders have incorporated the recurrent selection method in their conventional breeding programmes, as a new tool to achieve their diverse breeding objectives. Recurrent selection and traditional breeding have been used in a complementary way. This innovating breeding method has created a great deal of interest and anticipations among rice breeders for the development of rice varieties with increased yield, better resistance and greater stability.

Population improvement

The success of recurrent selection has led to several population improvement schemes. Recurrent selection has been applied to closed genetic systems *i.e.,* it was applied to genetically heterogeneous population of plants but no new germplasm was added to the population during the period when the procedure was being used. The potential limitations on progress from recurrent selection in closed populations have led to several proposals collectively known as 'population improvement' (Frey, 1984).

Eberhart, Harrison and Ogada (1967) proposed to comprehensive breeding system for both allogamous and autogamous species. Jensen (1970) proposed the 'diallel selective mating' (DSM) system which was designed primarily for autogamous species. By this procedure the breeding populations of plants seen as a dynamic gene pool (a) to which new sources of germplasm are introgressed whenever feasible (b) in which frequencies of favourable alleles are progressively increased via recurrent selection (c) in which genetic recombination is enhanced by massive hybridization among selected genotypes or in other words there is opportunity form multiparental gene recombination (d) from which cultivars, inbreds or parental lines can be extracted at any stage (Fig. 7).

• In diallel selective mating (DSM) the breeder select the parental lines and crosses them in a diallel series (Column-1) and F1s of the diallel series are used to produce F_2 seed for raising F_2-F_6 generations.

• The F_1's are crossed ina convergent crossing programme to incorporate multiple parents (column-2). The F1 of the multiple crosses selfed to produce F_2 population and mass selection practiced among F_2 plants.

• The selected F_2 plants are intermated to produce 1st selective mating series Column-3).The remaining mass selected F_2 platns are selfed to produce bulk of F_3 generation.

• The F_1s of the mass selected F_2 (product of 1st mating series) selfed to produce a bulk of F_2 and some are selected for intermating to form the 2nd cycle mating series (column 4).

• Others are back crossed to other parents not included in the orginal diallel. Thus, this system is a unique method of combining conventional breeding methods and also permits additional recombination by intermating selected genotypes.

This system provides

• Conventional bulk population breeding for the biparental diallel crosses (coloumn 1)

• Mass selection in each population series (all columns).

• Recombination of selected genotypes, extraction of new cultivars on parent material in each stage and intogression of new germplasm into breeding population at any time.

DSM seems to be formidable due to large number of crosses and requirement of enough F_1 seeds in each crossing cycle, therefore, Jensen (1978) suggested use of male sterility factor to facilitate crossing and growing of breeding populations in a specialized environment to maximize genotypic expression of the trait under selection.

This system of breeding method provides an ever present dynamic gene pool in which selection, increase frequency of favourable alleles, intermating

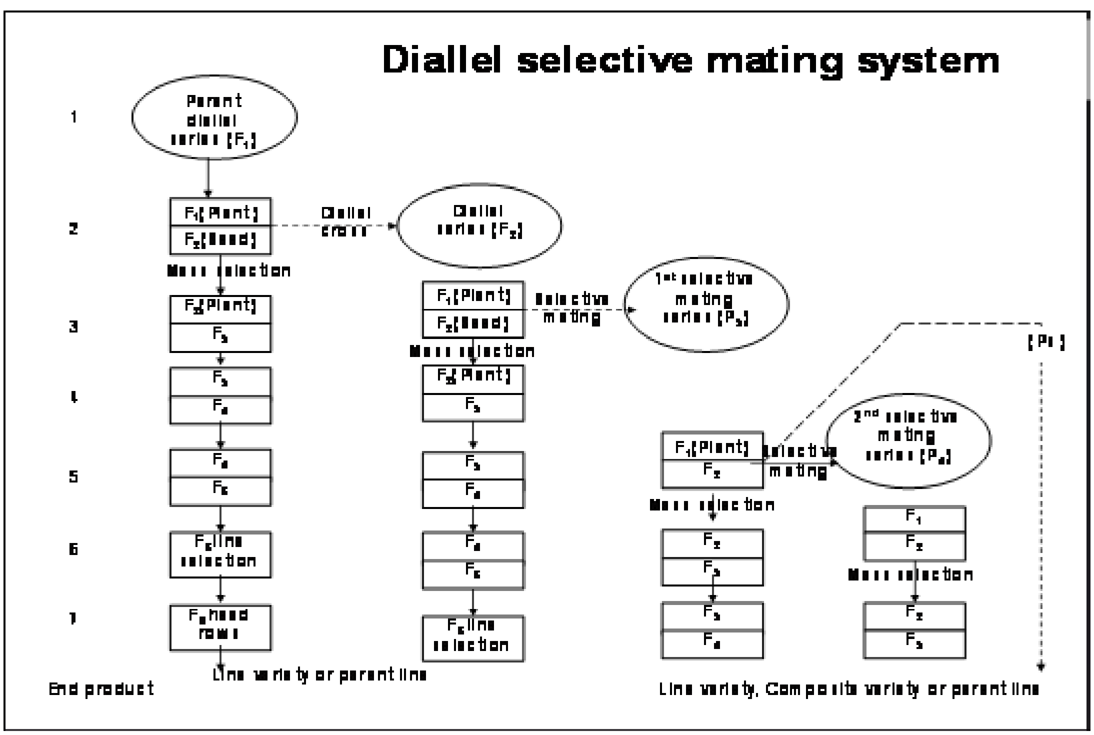

Fig. 7. Flow chart for the Diallel selective mating system (Jensen, 1978)

maximises the opportunity of recombination, opportunity exists to adjust gerplasm base by introgression at any time and useful agricultural cultivars could be extracted at any state of its evolution.

Unfortunately this method of breeding procedure has not yet been tested for its efficiency and efficacy in any crop plants and it is suggested to make use of this innovation to meet the time bound, goal oriented and diversified breeding objectives in rice.

VII. Scope for the development of heterogeneous population

There were four waves of genetic erosion and loss of genetic diversity in rice. During the early part of the rice breeding era 82 research stations spread over 14 states developed 445 varieties by improving native varieties through pure line selection of highly heterogeneous farmers varieties, which is treated as the first wave. The wide adoption of semi dwarf high yielding varieties again leading to sharp reduction of genetic diversity. Hybrid approach and use of same WA cytoplasm in majority of the hybrids brought about genetic as well as cytoplasmic uniformity in rice. Increased emphasis of molecular marker assisted back crossing of mega varieties may bring down genetic diversity as the fourth wave. Besides genetic uniformity the use of intensive monoculture in the agricultural ecosystem supported by intensive crop management, maximizes the spread and evolution of particular pathogen and pests and minimises the yield potential of crop varieties under different environmental stresses. Heterogeneous crops and cropping systems in subsistence agriculture avoids these problems but they often not been developed to maximize yield potential.

The use of planned heterogeneity in modern crop varieties was proposed by Rosen (1949), modified by Jensen (1952), and was first implemented by Suneson (1968), by releasing 'Harland' barley variety in USA. This variety emerged from his pioneering studies on bulk hybrid population and was the 28th generation seed lot of his famous composite cross bulk. To provide a combination of uniformity of agronomic traits and heterogeneity for disease resistance, Jensen (1952) proposed the use of multiline varieties. But the actual credit for conceiving a variety in a composite or synthetic form in self-pollinated crops goes to Norman Borlaug who has been instrumental in developing a comprehensive programme for producing multiline varieties of wheat (Borlaug, 1959). He proposed to blend eight to sixteen isogenic lines, each with different rust resistant allele, into a phenotypically uniform multiline variety which provides a sort of 'genetic resilience' against the disease appearing in epidemic form. Multiline breeding if properly conceived, organized and applied with different degree of sophistication can help to achieve diverse breeding objectives including high yield and stability over varied agrocliamtic conditions (Borlaug, 1981).

However, due to technical difficulties in production and maintenance of isoline mixtures and their susceptibility tonon-target diseases, this excellent theory of diversification of resistance against diseases was not properly executed. Wolfe and Barrett (1977, 1980) proposed that the variety mixtures due to their alleged advantage with respect to pathological and agronomic properties, can substitute the multilines and simultaneously retain the valuable features of a heterogeneous population for higher yields and stability.

Due to wide differences in agronomic uniformity and differences in various quality characteristics of the component varieties, the mixtures of varieties with several advantages over multilines were not commercially exploited. When multilines have so many undesirable side effects because of their uniformity and when lack of uniformity is the disadvantage of variety mixtures, then probably the ultimate use of intra-varietal heterogeneity would be settled with mixture of related lines (Groenewegen and Zadoks, 1979; Frey, 1982).

Besides all other advantages of growing mixtures, the hopes for benefits from mixed population mainly include improved grain yield. The expression of yield in mixtures maybe over compensatory, giving higher yields than the expected on the basis of component cultivars; compensatory giving yields similar to the mean of their component or under compensatory yielding less than expected is reflected by several complicated interactions between the constituent pure lines. Basically the magnitude and direction of this intergenotypic competition reflect the feasibility of composite breeding approach to crop improvement. Studies carried out in rice and various other crops had led to the emergence of three major views on the nature of relationship between competitive ability and agronomic superiority of the genotypes in the mixed population, *viz.,* no consistent relationship (Frey, 1967; Baker and Briggs, 1984); a strong positive relationship (Spitters, 1979; Valentine, 1982) and strong negative relationship (Jennings and Herrera, 1968; Khalifa and Qualset, 1974). Thus the effect of intergenotypic competition in bulk or mixed populations can be a serious problem, if the population is not managed through appropriate selection and may and up with reduced yield, vigour and plasticity.

A homogeneous composite variety constituted by mixing phenotypically similar but genotypically different related lines helps to maintain substantial amount of genetic diversity in such populations as well as expected to give longer varietal life with higher yield and greater stability of production through an optimum level of residual heterozygosity and positive intergenotypic interaction between the component lines of the population. There are several instances to demonstrate that the longevity and stability over varied environments of a variety depend on the extent the variety was homozygous at the time of its release for general cultivation. The secret behind the success of the widely adapted miracle rice IR 8 is believed to be its limited heterogeneity at the time of its release. The other convincing evidence, in particular, comes from the evolution of commercial cultivars and breeding lines developed by the University of Sydney and North-West Wheat Research Institute wheat breeding programme. The cultivar "Gamenya" which has enjoyed great popularity among farmers for a long time in many areas in Australia, maybe attributed to the residual heterogeneity resulting from limited selection pressure. (Bhatt and Derera, 1973). The same theory holds good for the popularityof many land races as compared to their pure line selections. 'Mozhagohukulu' and 'Kartikai Samba' in their native forms, for instance, are preferred by the farmers of Andhra Pradesh and Tamil Nadu as compared to their pure line selections BCP-1 and ASD-7 respectively. Similarly 'Saruchinamali' in Orissa is still popular among the farmers than its pure lines counterpart T-141 released by the Department Agriculture years back. Until this century, farmers used land cultivars which even though more or less uniform for agronomic traits often were heterogeneous for disease reaction alleles. Coffman (1977) listed 14 district pure lines of oat selected from land cultivar 'Kherson'. Derivatives of Kherson differed not only morphologically but also in reaction to major oat disease,

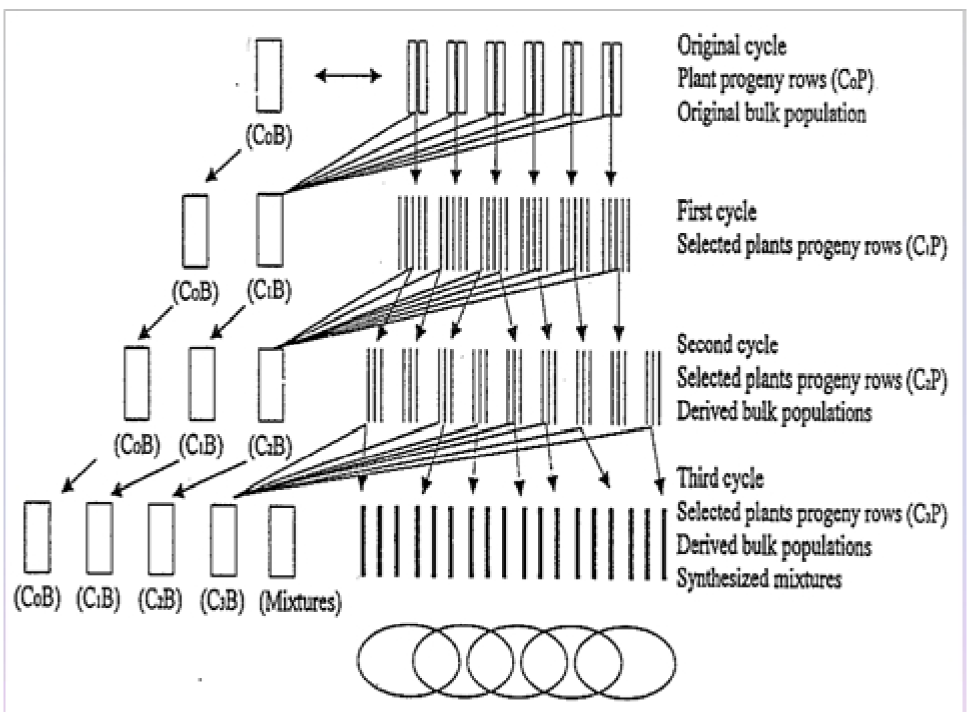

Fig. 8. Heterogeneous populations in rice

specially stem rust. Thus from the foregoing instances, it is obvious that limited heterogeneity in a variety maintained probably by low frequency of outcrossing among genotypes of the population, confers to it a sort of plasticity or a sort of genetic resilience to adopt itself to varied agro-climatic conditions.

Therefore, an attempt has been made to synthesize heterogeneous populations in rice by Das et al. (1990, 1998) Hasan and Siddiq (1990, 1995) by blending different morphologically similar lines that would interact harmoniously, an equilibrium between competitive ability and agronomic productivity can be realized. The synthesized populations, either in the form of mixture or bulks, and the progenies derived through pedigree selection indicated that although the mixtures were found to be superior to pure lines and the third cycle derived bulk (bulk or the selected fixed progeny rows) over the original base population (Fig. 8) indicated that there is enormous scope for intensive study to explore the possibility of exploitation of heterogeneous populations for realizing higher yield, greater stability of production, better agronomic uniformity and longer varietal life.

Considering the importance of heterogeneous populations for higher yield and stability a new selection approach is suggested which would combine both bulk population and pedigree mode of breeding systems to develop homogeneous mixtures for high yield and greater stability. The development of heterogeneous populations as a part of rice breeding programme as suggested would in no way be in conflict with production of new single pure line varieties but on the contrary would supplement such a programme. The prospective elite lines at the termination of selection cycles not only provide components for synthesizing heterogeneous population but also can be further evaluated and released as a highly homozygous and homogeneous variety.

CONCLUSION

While there are indeed many difficult challenges ahead in the 21st century, it is important to remember the importance of minor yield increases: 1% yield increase of a widely-grown variety will have a huge impact. Even in the advent of new promising technologies such as DNA markers, the time-tested conventional breeding and selection approaches will still account for significant improvement in increasing rice yields. A sound theoretical knowledge coupled with considerable hard work and long hours in the field are the secrets to breeding success, and this is likely to be the case for many years to come. The success and sustenance of rice breeding tells that there is no easy way to improve rice production, it demands patience, dedication, continuity and our total physical and mental commitments to field work (Das, 2013).

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