Recurrent Selection by Using Genetic Male Sterility for Rice Improvement

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Introduction

Rice breeders often encounter the situation in which it is very difficult to recombine desirable agronomic traits of different genetic sources and there is no room to choose other sources. These difficulties are supposedly arisen from genetic linkage or pleiotropy. However, as far as linkage is concerned, it is highly possible to break it up by some breeding techniques.

Recurrent selection seems to be a very effective breeding technique to dissipate undesirable linkage and to increase desirable gene combinations in a population. This technique, however, has been exclusively used upon cross-pollinated crops. There is no reason to exclude its use upon self-pollinated crops. The principal handicap in using recurrent selection upon self-fertilized crops like rice is the difficulty to make random crossing for recombination in each recurrent cycle.

The present paper proposes a new breeding technique, that is, recurrent selection using a male sterile factor, to overcome the difficulty imposed by undesirable genetic linkage for rice improvement.

Genetic recombination under selfing and random crossing

Under self-fertilization, only stable equilibrium is complete fixation. Suppose a monogenic difference between two true-bred parents, a half of F_2 segregants are homozygous and the other half heterozygous. From the deterministic point of view, heterozygosity is reduced to half in each selfing generation. Then the frequency of heterozygotes is expected to be $(\frac{1}{2})^{n-1}$ and that of homozygotes to be $1-(\frac{1}{2})^{n-1}$ in the n-th generation of selfing (F_n). Linkage serves to accelerate the approach to homozygosity.

This rapid approach to homozygosity under selfing is a serious barrier to produce new recombinants because the parental genotypes constitute a major portion of the hybrid population. The restriction of recombination imposed by rapid fixation in a selfing species may be minimized through the use of genetic male sterility.

Fig. 1 shows in what situation effective recombination occurs. In the case of digenic

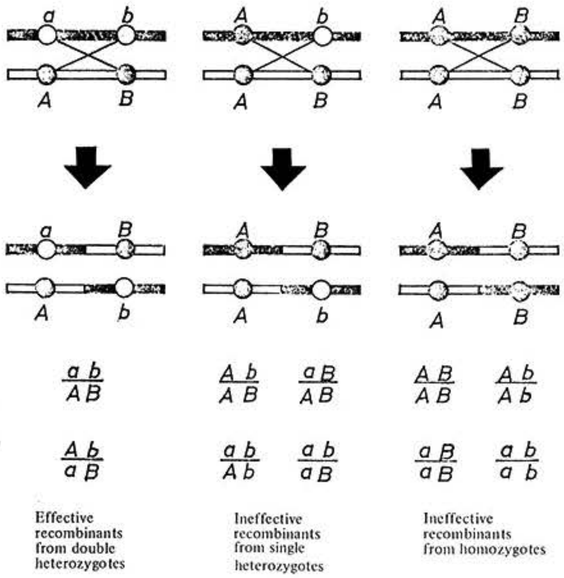

Fig. 1. Genotypes which produce effective or ineffective recombinants in the case of digenic linkage

Table 1. Expected lengths of initial chromosome segments under selected mating systems (Hanson, 1959)

Mating system (Generation)	Equivalent chromosome length	Expected length of initial linkage block
Single cross (F_1 gamates)	$s'=s$	$E(c)=1-e^{-s}$
Selfing (F_∞)	$s'=2s$	$E(c)=\frac{1}{2}(1-e^{-2s})$
Random cross (RC_nF_1)	$s'=ns$	$E(c)=\frac{1}{n}(1-e^{-ns})$
General formula		$E(c)=\frac{s}{s'}(1-e^{-s'})$

Note $s=E(x)=xP(x)$, x represents no. of breakup points appearing on the chromosome.

linkage, only double heterozygotes (left in the figure) produce new recombinants when a crossing-over occurs between the two loci, but single heterozytotes (center) and homozygotes (right) do not provide us with any new recombinants. This is the reason why loci have to be held heterozygous in a large proportion in order to increase opportunities to produce new recombinants.

The frequency of heterozygotes in a large random crossing population is expected to be 2 pq, where p and q represent frequencies of alleles in the locus concerned. It remains unchanged in the Hardy-Weinberg's equilibrium and is maximized in the case of $p=q=0.5$, that is the case in which the hybrid population is derived from a cross between two inbred parents. Random crossing is advantageous to promote genetic recombination since heterozygosity is kept in a large proportion.

Hanson (1959) has developed excellent theories relative to the breakup of initial linkage blocks under various mating systems. The length of a chromosome(s) is defined as an expectation of breakup points due to crossing-over appearing on the chromosome. The other special term employed in his theory is the equivalent chromosome length(s'), which represents the accumulated number of breakup points occurring on the chromosome during a certain number of generations under a selected mating system. The summarized results of the mathematical derivation are presented in Table 1. According to this theoretical investigation, random crossing among poly-parental progenies is very effective for shortening initial linkage blocks. In other words, recombination is remarkably promoted by continuing random crossing among progenies obtained from polycrosses between various parents.

Some experimental evidences have also been obtained relating to effectiveness of random crossing for advancing recombination in hybrid populations of self-pollinated crops such as cotton (Miller and Rawlings, 1967; Meredith and Bridge, 1971).

Recurrent selection by using genetic male sterility

Recurrent selection is a breeding system aiming at increasing the frequency of desirable genes and genotypes in a plant population. The obstacle to utilize this technique to improve self-pollinated crops is the difficulty to make random crossing for the recombination. This difficulty may be conquered by the use of genetic male sterility.

The effectiveness of the use of a male sterility factor to increase outcrossing was demonstrated with barley populations (Jain and Suneson, 1963). Recurrent selection using male sterility was suggested by Glimore (1964) for the improvement of naturally self-pollinated species. Application of genetic male sterility to recurrent selection was also proposed with such crops as sorghum and soybean (Doggett and Eberhart, 1968; Brim and Stuber, 1973).

In the case of rice, no useful allele for male sterility had been available. Male sterile mutants, however, were artificially induced by the gamma ray irradiation of the ^{60}Co sources and a chemical mutagen ethyleneimine (Fujimaki et al., 1977). Male sterility of these mutants was shown to be affected by a single recessive allele and useful to establish a random crossing population.

Fig. 2 presents a model of recurrent selec-

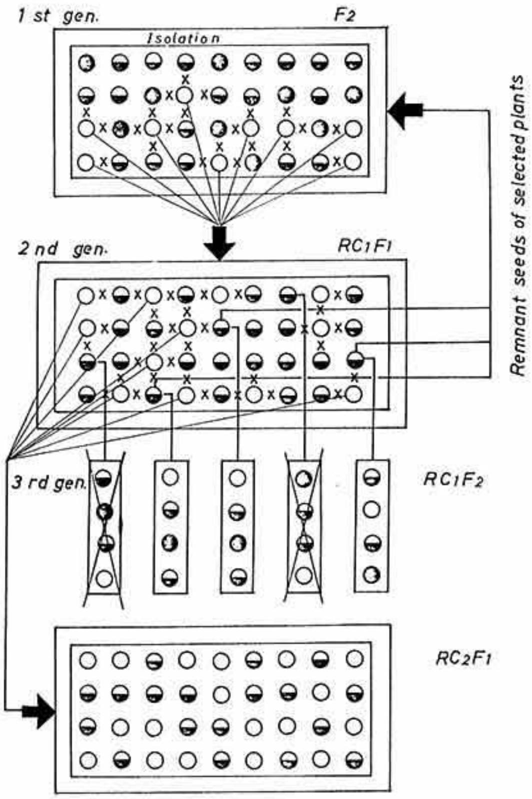

Fig. 2. Recurrent selection scheme using a recessive male sterile allele)
○ Male sterile ◒ Heterozygous fertile
● Homozygous fertile

tion by using a recessive male sterile allele. A breeding program is initiated by establishing a foundation population to which selection is to be applied. The population is composed so as to be segregating for male sterility. It can be derived from various sources such as biparental single crossing, double crossing, polycrossing or diallele crossing. We grow it in an isolated environment and advance outcrossing between male sterile plants and fertile ones. By collecting seeds from male sterile plants, we can obtain a random crossed population. At least 2–3 cycles of random crossing are required for advancing recombination within the foundation population before initiating selection.

In the random crossing phase, mild mass selection might be applied to the population. But intensive selection should be avoided especially to highly heritable characters since it may incur the increase of homozygosity, and the chance of free recombination may be reduced. Another point to be kept in mind is how to do with selection for flowering time. Flowering time is usually a highly heritable character to which intensive selection should be avoided. But selection for this character is essential to synchronize flowering in order to advance random crossing in the population. Under these circumstances, however, it is desirable to apply selection to flowering time in an early generation since opportunities of outcrossing between plants differing in flowering time seem to be very rare in any generation.

In the selection phase of recurrent cycle, selfed seeds are harvested from fertile plants to develop S_1 progenies. A part of selfed seeds of each plant are reserved for later use and the other part are used for S_1 progeny test. Every S_1 line is supposed to segregate for male sterility in a monogenic ratio. Therefore it is difficult to evaluate agronomic traits relating to seed production like yield, but such agronomically important traits as grain quality, resistance to various disease and insect pests, cold tolerance, plants type, culm strength and leaf senescence are able to be tested by using S_1 lines.

Based on the results of S_1 progeny tests, S_1 lines with desirable traits are selected. If there are some promising lines for practical use, they are continuously self-pollinated with selection to fixation. Unless any promising line is obtainable, S_1 lines excellent in some agronomic traits are marked and reserved seeds of their parental plants are mixed up to compose another foundation population for further recurrent selection. Recurrent selection is repeated to increase the frequency of desirable genes and gene combinations until some plants carrying practically satisfactory traits appear in the hybrid population.

The model of recurrent selection will be modified in various ways. For instance, when we wish to introduce any new trait not involved in the original parents, we can utilize a new variety carrying the trait concerned at any cycle of recurrent selection by interplanting it in a random crossing population. The amount of gene flow from the new variety is able to be controlled by adjusting the mixing proportion. At an extreme case where all self-fertile plants are replaced with a recurrent parental variety, the breeding scheme becomes equivalent to the backcross system proposed by the present author (Fujimaki, 1978).

Discussion and conclusion

Three disadvantageous features of conventional breeding systems for the self-pollinated crop improvement have been pointed out by Jensen (1970). They are (1) the limited size of the gene pool utilization (usually two parental crosses), (2) the restrictions of genetic variability and recombination potential through intensive inbreeding and (3) the absence of intercrossing among hybrid progenies.

There are opportunities of effective recombination in F_1 meiosis but few chances of recombination are expected in advanced generations because homozygosity rapidly increases through self-fertilization. Genetic recombination between linked loci is restricted to a great extent in the conventional breeding techniques of self-pollinated crops.

Recurrent selection is considered to be excellent breeding system to cover these disadvantages in the conventional techniques. A model of recurrent selection for rice improvement has been proposed in the present paper. A recessive allele for male sterility induced by artificial mutation is effectively utilized to compose a random crossing population. This new technique will be extensively applied to rice improvement when undesirable linkage exists between agronomically important traits, or when useful alleles are to be brought together from various genetic sources.

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