On the Advances of Plant Breeding

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Introductory remarks

By exploring the path plant breeding has followed, we would like to foresee where it will lead to in the future. Plant breeding has gradually advanced since the time when the so-called "old expert farmers" made efforts to introduce and cultivate various new crops. After the discovery of the law of heredity (Mendel, 1866), it has made great progress with the help of wide-range researches on induced mutation, cytogenetics and gene action. Moreover, new facts have recently been brought to light which could not have been conceived from classical genetics. So the need pressed a new field of plant breeding to be established and breeding was to be seen in a new light. This view is accepted usually in Japan, and in most other countries of the world plant breeding probably has followed the foregoing path or will pursue a similar one in the future.

1. Genic breeding

Since the rediscovery of Mendel's law (de Vries, Correns, Tschermak, 1900, respectively), genes have become an improtant aspect in plant breeding. At first, better strains were produced solely by collecting various strains, then crossing them with one another. Later on induced mutation came to be available in plant breeding. On the other hand, collection and preservation of various genes of different species have become one of the important fields of plant breeding (Vavilov, 1926).

(1) Breeding by separation

In the early days of plant breeding, only strains which appeared to be good were cultivated, then it was found that the better strains could be selected by collecting many local strains and by comparing them with one another. Soon after the rediscovery of Mendelism, however, it became clear that the so-called local strains consisted of various lines. Johannsen (1903, 1909) demonstrated in his pure-line theory that no selections would work in a pure line. Resting on this theory, a lot of attempts have been made to segregate better pure lines from good but heterogeneous local strains, and actually many excellent strains have thus been produced.

(2) Breeding by hybridization

As there was a limit in improvement of plants by the separation breeding, it gradually

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became popular to breed excellent strains by recombining genes based on Mendelism, and continues today as a major current of plant breeding. A great number of works have accumulated with regard to methods and theories of hybridization and fixation of genes. Especially, such subjects as incompatibility (Correns, 1912), photoperiodism (Garner and Allard, 1920), embryo culture (Laibach, 1925), polygenes (Mather, 1949) and others have developed intensively. The recent achievements in breeding by hybridization are represented in Dr. Borlaug's efforts against the starvation of humankind for which he was awarded a Nobel peace prize in 1970, where he brought some Mexican strains of common wheat which had been improved in Mexico (Borlaug, 1968). They had the characteristics of short culm and long ear acquired from Japanese wheat strain, Norin 10.

(3) Induced mutation

Since Muller (1927) succeeded in inducing artificial mutations by X-rays, various mutagens have been tested to find their ability to induce useful mutant genes, some of which came into extensive use in plant breeding. Breeding by mutations has been carried out on a large scale at the γ-field in Brookhaven, U. S. A., since 1947. Japan also constructed a γ-field at Ohmiya-cho, Ibaraki Prefecture in 1961. Breeding by induced mutation, which might be related to one peaceful use of atomic energy, is being pursued with the aid of varions facilities. Gaul (1963) reviewed the works on mutations in plant breeding. Gustafsson's studies on barley (1963) attract our attention. Since Auerbach et al. (1947) and others started research on mutations by chemical mutagens, studies have been carried out by many investigators up to the present where they are elucidated in terms of changes in gene coustitution. Breeding by induced mutations are being explored at various research institutes of many countries.

2. Chromosomal breeding

The discovery of linkage (Bateson et al., 1906; Morgan, 1917) enabled the consideration of chromosomes as the carriers of genes, and the finding of sex chromosomes resolved many puzzling problems of genetics. Furthermore, the advances of the study on polyploidy gave suggestions regarding the practical use of polyploids for plant breeding, an example is the increase in size and amount of a particular content of polyploid cells. The application of triploids in the production of seedless fruit attracted public attention. Plant breeding was advanced further, attaining to make use of haploidy and chromosomal translocation.

(1) Polyploidy

The study on polyploidy started in *Chrysanthemum* (Tahara, 1921) and *Triticum* (Kihara, 1924), and was intensively developed by Prof. Kihara in a series of works on genome analyses of *Triticum* and *Aegilops* (Kihara and Nishiyama,1930; and others). Synthesis of new species or allopolyploids (Karpechenko, 1928; Kihara and Katayama, 1931; and others) and production of autopolyploids (Nishiyama, 1947; Müntzing, 1951) were the typical application of polyploidy to plant breeding. An increment of sugar content of sugar cane was achieved by increasing the chromosome number (Bremer, 1923; and others). Triploid plants bearing seedless fruit (Kihara and Nishiyama, 1947) and triploid sugar beets (Matsumura, 1953; Mochizuki, 1953) were produced and put into practical culture. In medicinal herbs, chromosome doubling was also attempted to increase some useful ingredients (Suzuka, 1958). Müntzing (1957) reviewed the works on plant breeding relating to polyploidy. Concerning the wheat genetics including polyploidy, an international symposium has been held every five years since it arose with Prof. Kihara as leader (Japan) in 1958,[1] and WIS (Wheat Information Service) has been issued since 1954 with Prof. Kihara as chief editor.[2]

(2) Haploidy

Subsequently, the haploid method (Katayama, 1950; Katayama and Tanaka, 1969) was introduced into plant breeding, which rested on an assumption that pure homozygotes would be obtained by doubling the chromosomes of haploids. This method developed in tobacco (Tanaka and Nakata, 1968), has extended to various kinds of crops. The study of the haploid method stemmed from the induction of a considerable number of haploids in *Triticum monococcum* (2n=14, genome formula AA) by means of pollination with X-rayed pollen (Katayama, 1934) and also from the findings of colchicine method in doubling chromosomes (Blakeslee and Avery, 1937). The haploid method has been established in tobacco where anther culture enables the production of haploid plants in large numbers. Haploid breeding in rice plants has also been developed as intensively as in tobacco (Niizeki and Ohno, 1968). Katayama and Nei (1964) and others reviewed the researches on haploidy. In recent years the study on haploidy has become so extensive that HIS (Haploids Information Service) with Prof. Melchers as chief editor made its first appearance in 1972,[3] and the first international symposium of haploids in higher plants was held in Canada with Prof. Kasha as leader in 1974.[4]

(3) Translocation and aneuploid

Recently it became possible to produce new varieties with different genic constitutions resulting from the exchange of whole chromosomes or of parts of chromosomes between different genomes. This method is favorable for plant breeding because it exchanges only the chromosomes or the parts concerned without affecting other gene constitution, forming a remakable contrast in this respect with breeding using mutagens. In plants, Yamashita (1950) experimentally produced a chromosome ring consisting of 14 chromosomes in *T. monococcum* using translocations induced by X-rays. Tazima (1944) already

1) The first symposium was held at the University of Manitoba, Winnipeg, Manitoba, Canada and this proceedings was edited by Prof. Jenkins.

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3) Max-Planck-Institut für Biologie, Tubingen, West Germany.

4) The first symposium was held at the University of Guelpf, Guelpf, Ontario, Canada and this proceedings was edited by Prof. Kasha.

succeeded in translocating the genes for egg color of the silkworm on the sex chromosome. The translocation is utilized for the sex identification of the silkworm in the egg stage. The researches on aneuploids of wheat by Sears (1954) proved to be the basic achievements in this field forming the foundation of the so-called chromosome engineering. Mochizuki (1961) discussed on the gene introduction from related species of wheat. It is also interesting that Nishimura (1961) tried to do gene analyses of rice with the aid of translocations.

3. Physioecological breeding

Although the purpose of the genic and chromosomal breedings is to obtain excellent strains with fixed genotypes, physioecological breeding does not neccessarily aim at fixed genotypes, but at making use of excellent phenotypes even if they are temporary; from a practical viewpoint, an improvement even in one generation could meet the purpose of the breeding.

(1) Heterosis

In the course of breeding by hybridization, a phenomenon known as hybrid vigor (or heterosis) was found; F_1 hybrids between different strains showed a greater viability than either of the parents did. Hybrid vigor was studied regarding the breeding of the silkworm in Japan (Toyama, 1906) and in America it has been applied to the practical production of corn. Concerning heterosis, Jones (1917) and others gave various working hypotheses. On account that a uniform vigor manifestes only in F_1 generations, yearly production of hybrid seeds by artificial crosses is indispensable for the usage of hybrid vigor. To save hand labor needed for emasculation in the production of hybrid seeds, use of male sterility was highlighted and extensively investigated (Jones and Clarke, 1943). Hybrid seed production was also discussed in wheat and rice using the male sterility caused by the alien cytoplasms (Kihara and Tsunewaki, 1964; Tsunewaki, 1969).

(2) Cutting and grafting

Cutting and grafting, which have been employed for the vegetative propagation of good strains since former years, take the advantage of physioecological phenomenon of plants. A lot of researches have been conducted on the rooting of cuttings. Grafting puts two different plants in a symbiotic state where the scion is subject to various influences such as not seen when it is independent (Winkler, 1907; Baur, 1910; Imai, 1936). Although it might be explained in terms of graft hybrid, the phenomena are thought to be ascribed chiefly to the transfer of some components in the sap from the stock to the scion. In connection with this, however, study on protoplast fusion, which will be described later, might make a fresh development. Cutting has been an important part of tree breeding, and grafting has been as important as pruning in pomiculture. Recently, grafting has been extended to the production of fruit vegetables to endow them with resistance to diseases and insects.

(3) Resistance and environmental control

Acquisition of resistance to diseases and insects has been a major object of the study on resistance of plants; it has been worked out by selecting suitable stocks for grafting, and lately by breeding of resistant varieties to various diseases and insects. Even though a resistance of a variety can be attributed eventually to its genotype, it is supposed to be greatly conditioned by the mode of physioecology of plants. More studies, therefore, are expected in this respect. Prof. Hemmi (1949) was engaged in this subject in his study on rice blast. Stakman and Harrar (1957) dealt with this subject in general.

It has become popular to increase the yield of crops by controlling the environment, for example, irrigation cultivation and greenhouse culture. Recently, it is called horticulture under structure. Illumination culture taking the advantage of photoperiodism of plants is a good example. Artificial coloring and growth control by chemical sprays can also be regarded as good examples, and hormones have become applied extensively to grapes and other plants in the production of seedless fruit.

4. Breeding in new fields

Although the achievements in plant breeding so far mentioned were gained by keeping in step with the advances of breeding methodology, there has lately occurred such a rapid progress in the biological field leading to new aspects of breeding that could not have been imagined from previous knowledge of biology. We intend to refer to the new fields of biology in cell culture, protoplasts and plasmids considering their connection with plant breeding.

(1) Cell culture

Tissue culture using animal material has long been carried out, and has recently extended to plant material. Study on tissue culture using plants is presently flourishing, and Steward et al. (1958) have at last succeeded in culturing single cells and in redifferentiating intact plants from them. Cell culture is expected not only to become a powerful approach to the understanding of cell differentiation from a single fertilized egg cell into an individual, i. e., morphogenesis, but a revolutionary means for future agriculture, namely starch production by culture of single cells with chloroplasts in tanks not depending on earth, may also become possible. Recent forage production from Chlorella culture can be considered as leading in the way (Tamiya, et al. 1953).

(2) Protoplast

That a hybrid of higher plants could be produced without involving a normal sexual cycle, by simple fusion of two naked cells or protoplasts isolated from different species (Carlson et al., 1972) as is now understood could not have been hinted a short while ago. Study on the protoplasts of higher plants started with the use of some degrading enzymes for the isolation of protoplasts (Cocking, 1960). Many possible advantages of protoplasts were appreciated with respect to plant breeding, such as the production of numerous mutants in a Petridish, parasexual hybridization through cell fusion and regeneration and so forth (Takebe, 1975). Development in this new field is expected.

(3) Plasmids

Bacteria are the most favorable organisms for genetic researches because of their haploid genome which enables a mutation to manifest immediately, and of their very short life cycle. Genetics of plasmids has especially been developed remarkably using bacteria, mainly the colon bacillus. Plasmids which carry some genetic information behave independently of ordinary genomes and will become a powerful means for the gene engineering. The study of plasmids may lead to the understanding of life, and moreover to the creation of new life which would be the ultimate goal of breeding. This study originated from the works with *Neurospora* by Beadle (1945), and has been promoted by Lederberg et al. (1952) and others.

Closing remarks

We have described the progress of plant breeding made gradually from what is called "seed selection", and referred as far as to the subject of life itself. Our daily efforts after the truth are expected to be put to practical use and to make the nature of life clearer.

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