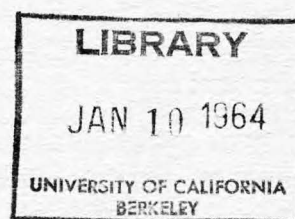


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CANADIAN JOURNAL of GENETICS and CYTOLOGY

Journal Canadien de Génétique et de Cytologie



VOLUME V

**DEC. 1963
DÉC.**

**NUMBER 4
NUMÉRO**

**Published Quarterly by
The Genetics Society of Canada**

**Revue Trimestrielle de
La Société de Génétique du Canada**

THE GENETICS SOCIETY OF CANADA

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ANALYTIC BREEDING IN *SOLANUM TUBEROSUM* L. — A SCHEME UTILIZING PARTHENOTES AND OTHER DIPLOID STOCKS

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Analytic breeding (Chase, 1962) is a three phase process involving, a) reduction of a polyploid to its diploid components, b) intensive breeding and selection at the diploid level, and c) resynthesis and testing of the polyploid form. The common potato, *Solanum tuberosum* L., an autotetraploid (Cadman, 1942), affords unique opportunities to the breeder interested in this radical approach to the problems of intergenomic and intragenomic repatterning in polyploids. The potato can, with comparative ease, be a) propagated vegetatively, b) reproduced sexually, c) reduced to the diploid state by parthenogenesis, d) crossed with diploids including native forms at the diploid level, and e) polyploidized.

In their pioneering studies of parthenogenesis in the common potato and of cross and self fertility of potato haploids, R. W. Hougas, S. J. Peloquin, and their associates, A. C. Gabert, and R. W. Ross, (see papers of these authors, 1957 through 1962) have gone far towards demonstrating the feasibility of the analytic approach to potato improvement. In their discussion of 'the potential of potato haploids in breeding and genetic research', Hougas and Peloquin (1958) have presented many of the arguments for genetic and breeding studies at the diploid level. (In the subsequent discussion, the word 'haploid' will be avoided, because, in the opinion of the author, the duality of meaning of the word leads to confusion. Thus, haploid is the lowest term of the genomic series haploid, diploid, triploid, tetraploid, etc.; it is also correctly applied to an entity with the gametic chromosome number. In polyploids, where these meanings do not coincide, ambiguity results from the use of the term.) By outlining the steps of a hypothetical breeding scheme in the presentation below, an attempt will be made to show how polyploid and diploid forms may possibly be manipulated to advantage in a commercial potato improvement program. Concisely, the purpose of analytic breeding is to reverse the evolutionary pathway, from polyploidy back to diploidy, in order to intensify selective breeding and to set the stage for retracing the evolutionary sequence from ancestral diploidy to polyploidy with genomes molded more closely to current human needs.

In the commercial potato, the breeder's variety is a single elite plant, expanded vegetatively into a clone. In evolutionary and commercial competition, heterozygous tetraploid forms of the potato have come to the fore. For this reason it is assumed here that both heterozygosity and tetraploidy confer advantages *per se* in the potato.

Plant breeding involves two rather dissimilar efforts. These are, a) the upgrading under selective pressure of basic chromosome sets, and b) the fitting together of whole chromosome sets in physiologically effective diploid or

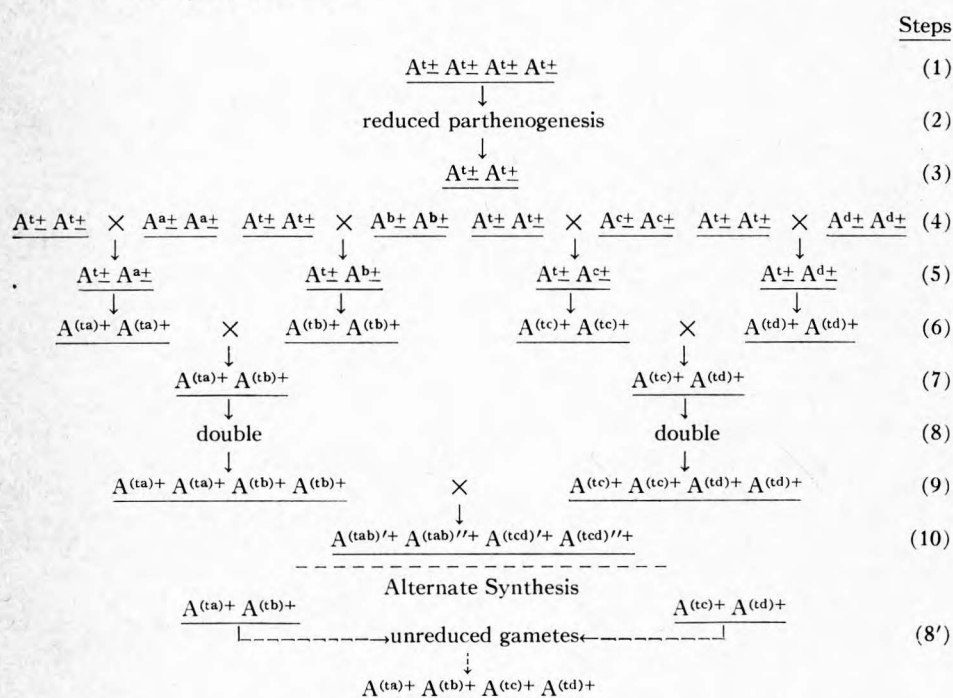
Manuscript received June 24, 1963.

Can. J. Genet. Cytol. 5: 359-363. 1963.

polyploid systems. In diploid crossbreeding crops such as maize, the refashioning of the sets, or genomes, is accomplished through various forms of close breeding such as inter-mating selected individuals, selecting recurrently in large populations, backcrossing, and, most characteristically, by selective selfing. The fitting together of pairs of genomes is determined by test crosses and culminates in the formation of a heterotic F_1 hybrid. In potato, and in other polyploids, improvement has been inhibited by the difficulty of separating these two phases of breeding. The basic difficulty in refashioning individual genomes of autopolyploids stems from the discouragingly slow rate at which homozygosis is achieved upon inbreeding (Burnham, 1962). Yet, in order to gain full efficiency in intragenomic selection, one must first stabilize the genotype by inbreeding or some equivalent process.

A Hypothetical Analytic Breeding Scheme for the Common Potato

In Fig. 1 the ten principal steps of a *hypothetical* analytic breeding scheme for the potato are presented. Those steps which have been successfully demonstrated are indicated by solid lines; those presenting some uncertainty are indicated by dashed lines.



Key: A = potato genome
t = gene system from tuberosum
a = gene system from diploid species or selection
b = gene system from diploid species or selection
c = gene system from diploid species or selection
d = gene system from diploid species or selection
+ = favorable genes
- = unfavorable genes
0 = a recombination of genes
', '' = gene system altered by crossing over

Fig. 1. A hypothetical analytic breeding scheme for the common potato.

The first operation, step #1, is the selection of the source material, that is, the clone or set of clones of the commercial potato best combining breeding quality with the possibility of obtaining fertile diploid parthenogenetic derivatives. Through reduced parthenogenesis, step #2, a series of diploid derivatives of the tetraploid source is created. Hougas, Peloquin, and Ross (1958), and Gabert, Hougas, and Peloquin (1962) have developed techniques for control of this process and have already produced a substantial number of parthenotes. Next, step #3, comes the selection and clonal propagation from among the array of parthenotes of one or, preferably, several plants that combine self and cross fertility with vegetative vigor and agronomic worth. This is followed by step #4 wherein the selected parthenote or parthenotes are crossed to a series of diploid species, varieties or selections. In the diagram, four crosses, for development of four improved sets of chromosomes, are indicated. The objectives at this stage are to improve each of these four or more sets separately while concurrently increasing their heterotic diversity. It may be feasible to work entirely with the immediate parthenogenetic derivatives of experimental and commercial potato varieties at this stage, or it may prove to be more productive to intercross the derivatives at the diploid level, or to cross these parthenotes with diploid species. Furthermore, some parthenotes may prove to be adequate without genic supplementation and some existing native diploid forms may find use directly in the breeding program. Crosses of potato parthenotes with a number of diploid species have been made and the F_1 progeny are remarkably vigorous (Hougas and Peloquin, 1959; Peloquin and Hougas, 1961; Ross, Peloquin, and Hougas, 1962). Indeed, the ease of crossing with native diploids, while helpful to the breeder, brings into question the present taxonomic treatment of the genus.

Inbreeding of the diploid F_1 crosses, step #5, with selection under appropriate stress, is required at this stage to fix desirable genetic material. Because self incompatibility and male sterility occur in the potato, close inbreeding may in some cases not be feasible. Backcrossing and further outcrossing is in order if required by the genetic objectives. Step #5 presents the plant breeder no problems of an unusual nature.

From the diploid strains, each previously inbred under selective pressure to homozygosity for genes controlling attributes of economic importance, four elite individuals are selected, step #6, for resynthesis of the polyploid. Preliminary test intercrosses and performance trials would presumably guide this selection. The first phase of resynthesis, step #7, is the crossing of the diploids in pairs, combining those members of the selected set of four that in testcrosses show the *weakest* heterotic interaction. The pairs demonstrating weakest heterotic interaction should be combined at this stage in order to maximize the heterotic interaction in the final combination, the genetic principle involved being similar to that which leads the corn breeder to combine the more closely related or less heterotic pairs of inbreds in the single cross parents of a double cross hybrid. These diploid hybrids are then manipulated to double their chromosome complements, step #8, and the two resulting tetraploids are crossed in turn, step #9, to establish the heterotic tetraploid hybrid.

An interesting alternative for resynthesis of the polyploid involves the recombination of unreduced gametes from the two diploid hybrids, alternate step #8'. (There is some indication that, in potato, unreduced gametes have

been subjected to crossing over before meiotic failure ensues, see Prakken and Swaminathan, 1952. If this should be characteristic of induced non-reduction, there would be less merit in this alternative scheme for resynthesis.) If the sets of chromosomes from each of the intermediate diploid hybrids can be 'captured' intact, then the fusion of unreduced gametes affords a means for bringing together the four unaltered parental chromosome sets and would, in the author's opinion, maximize the heterotic potential.

In respect to the functioning of unreduced gametes, there are a number of records (Prakken and Swaminathan, 1952) of tetraploid progeny in crosses of diploid by tetraploid. To bring two unreduced gametes together in syngamy is admittedly much more difficult. However, the technique of making pollinations and maturing seed on cut shoots of potato (McLean and Stevenson, 1952) greatly increases the opportunity for successful manipulation of the gametic processes, and, if unreduced pollen grains of potato can be recognized by size and separated for use in pollinations, the bringing together in syngamy of unreduced gametes should be feasible at the technical level. Simura (1956), following colchicine treatment of the microsporocytes of the tea plant, was able to distinguish pollen grains with unreduced gametes under low magnification and to separate these grains for use in pollinations.

The final breeding operation, step #10, of the hypothetical scheme is to multiply the resynthesized polyploid vegetatively and to test it as a commercial potato.

It is important to note that all of the operations outlined above except the theoretically ideal solution for resynthesis of the polyploid, alternate step #8', have in one or another line of research already been accomplished. Thus, it is not unreasonable to expect that these operations can be carried out in stepwise fashion as outlined.

Discussion

The nature of heterosis in potato and the consequences of polyploidy are of particular importance to the breeder. In terms of breeding objectives, certain forms of heterosis and of polyploid response may be undesirable, for example, increased plant size *per se*. As in other crops, the expression of physiological efficiency must be canalized. Because the potato crop is grown for its tubers, physiological efficiency, in order to have value, must be expressed in the form of increased yield and quality of marketable tubers.

Though the analytic method has been presented from the point of view of the plant breeder concerned directly with the development of commercial varieties, one should not lose sight of the opportunities to gain practical and theoretical information from a breeding effort of the type proposed. With the materials and manipulative skills such a breeding program would generate, there would be at hand unique opportunity for studying dosage effects, physiological relations of diploids and related polyploids, epistasis, the heterotic possibilities of multiple allelism, genetics of disease resistance, and the evolution of the modern potato.

Summary

For exposition, a hypothetical analytic breeding scheme for the common potato, *Solanum tuberosum* L., is presented. The principal steps are, a) reduction of the autotetraploid to the diploid level by parthenogenesis, b) intensive breeding and selection at the diploid level, and c) resynthesis of the polyploid.

The thesis is advanced that plant breeding involves, at the genome level, two distinct efforts, i.e., selection of favorable genes within individual chromosome sets and combination of whole sets in physiologically effective systems. Separation of the intragenomic and intergenomic phases of plant improvement, through application of the analytic method, affords the potato breeder opportunities for higher levels of genetic control than presently obtained.

Acknowledgements

The author wishes to express his thanks to the DeKalb Agricultural Association, Inc., for the leave of absence during which this paper was prepared; and to the late Dr. Donald F. Jones and his associates at the Connecticut Agricultural Experiment Station and to Dr. Francois Mergen of Yale University for helpful advice and assistance.

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