

POTATO IMPROVEMENT THROUGH PARENTAL LINE
BREEDING — A FIVE YEAR REPORT
OF THE NORTH CENTRAL 35 REGIONAL PROJECT, NC-35¹

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INTRODUCTION

A growing realization among North Central region potato breeders that better parents were needed to effectively continue varietal improvement led to establishment of the NC-35 regional project, "Potato Improvement Through Parental Line Breeding" in 1956. The proposal for the project was made by Rieman et al (3). The project was designed to bring about a concerted effort among breeders to develop clones *genetically* improved for certain desired characters.

The need for a project such as this is easily illustrated. Toxopeus (4) observed that methods used in potato breeding have remained essentially unchanged over the past century in spite of a rapid development in genetics and related disciplines. The emphasis, here and abroad, has been on practical breeding results; i.e., improved commercial varieties. Crossing of superior phenotypes and selecting from increasingly larger F₁ populations has resulted in many outstanding varieties. This method, however, and its variations, like open-pollinated corn breeding, is leading to a point of diminishing returns. Several reasons are apparent for this.

The cultivated potato, *Solanum tuberosum*, is a tetraploid species in a polyploid series ranging from 24 to 72 chromosomes. Its inheritance is therefore complex. The basic monohybrid ratio of 3:1 found in diploid plants becomes a 35:1 ratio in the cultivated tetraploid potato. As a result, inheritance of most economic characters in potato is undefined.

The number of economic characters in the potato has been estimated by several authorities as ranging from 20-30, which is a relatively large number compared to other crops. New advances by industry, particularly, the phenomenal growth of processing during the past decade, result in a need of additional characters in new varieties. The increasingly larger number of economic characters needed in new varieties poses a stimulating challenge to breeders. For example, if a character would be transmitted $\frac{1}{2}$ of the time by parents to their progenies, over one million seedlings would have to be grown on the average to obtain one individual having twenty desired characters (2²⁰), and over two million to obtain the one individual having twenty-one desired characters (2²¹). Populations of these magnitudes exceed total yearly capabilities of all potato breeders in the United States.

It is evident that a concerted and organized effort is needed to exploit all available possibilities in keeping pace with new demands. The framework for an organized cooperative program is provided for by NC-35

¹Accepted for publication January 29, 1962. Paper No. 1101 of the Miscellaneous Journal Series of the Minnesota Agricultural Experiment Station.

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or a similar project. The recent rediscovery and increase of 2n stocks of the cultivated potato by Hougas *et al* (1, 2) provides a possibility for conducting necessary basic genetic studies at the easier and more readily understood diploid level.

PROGRESS OF WORK AND PRINCIPAL ACCOMPLISHMENTS

The NC-35 project was activated in 1956. Seven stations, Indiana, Iowa, Michigan, Minnesota, Nebraska, North Dakota and Wisconsin have contributing projects. Of these, Minnesota, Nebraska and North Dakota have been receiving RRF funds. The Minnesota station acted as the coordinating station for the project.

The project has enabled the establishment of programs designed to produce parents improved for certain important economic characters. In general, emphasis has been placed on (i) general evaluation of available materials to identify stocks having the desired characters, (ii) concentration of genes conditioning the desired characters through appropriate crosses, (iii) screening of resulting progenies for several clonal generations to identify accurately clones having desired characters, and (iv) genetic evaluation of potential parents by suitable test progenies. Related studies include modes of inheritance of desired characters, nature of resistance, improvement of screening procedures, and evaluation of breeding methods.

Major emphasis has been given to development of parent clones having improved resistance to common scab, late blight, virus Y, or heat and drought. Some attention has also been given to yielding ability, virus X, tuber appearance, non-parasitic internal necrosis, specific gravity, chip color, or reducing sugar.

Common Scab:

Four sources of resistance, three from *S. tuberosum* and one from *S. phureja*, were used in programs to develop parents with improved resistance to common scab. Clonal resistance of parents was found to be reflected in their progenies. Parents in the two most resistant classes did not differ in ability to transmit resistance and also produced the most resistant progenies. Parents in the two more susceptible classes did not differ and produced less resistant progenies. Parents having no scab resistant ancestry produced the least resistant progenies. Progeny differences in levels of resistance from the three parent groups could be explained on the basis of a single gene having additive effects. At least two genes seem necessary for effective clonal resistance. Differences in sources of resistance did not seem important. In another study, however, heritability estimates suggested that resistance is conditioned by genes having both dominant and additive effects. Hence, both types of gene effects need to be considered in the development of parents with improved resistance to common scab.

Studies pertaining to reliability of testing procedures suggested that though the correlation between readings for two years was high, the phenotypic variance due to years was much greater than that due to replication, suggesting desirability of testing for several years. Levels of parent resistance were reflected in the degree of yearly variation observed in segregates. Variation in resistance ratings of segregates became greater as levels of parent resistance decreased.

On the basis of at least three years testing, 57 selections from crosses and 23 from self progenies have been identified as having a high degree of clonal resistance. It is probable that some of these are improved genetically for scab resistance, but necessary progeny tests have not been made as yet.

Late Blight:

Two types of resistance to late blight are available. Resistance may be highly specific, conditioned by qualitative genes conferring immunity to specialized races of late blight, or it may be generalized, controlled by multiple factors conferring "field resistance." Although the specific type is easier to work with, both in breeding and testing, new races of the pathogen can and do reduce the value of this type of resistance. On the other hand, the generalized type of resistance does not seem to be affected by variability of the pathogen.

Initially, "field resistance" in clones with and without immunity genes was studied. It soon became apparent, however, that data on field resistance of clones possessing immunity genes would be extremely difficult or impossible to interpret due to differences in aggressiveness of different late blight races and the problem of distinguishing the two types of resistance. Therefore, work involving clones with immunity genes was discontinued.

Three species, *S. tuberosum*, *S. andigenum*, and *S. demissum*, have been studied to develop parents with improved field resistance to late blight. The general level of field resistance found in *S. tuberosum* has been fairly low. Almost all selections with some clonal resistance have scab-resistant ancestry, suggesting that genes for field resistance to late blight may have a genetic association with genes for scab resistance. Though a number of progenies from clones with varying degrees of resistance have been tested, the mode of inheritance is still obscure. In general, segregations observed correspond to those expected for characters conditioned by multiple factors. Some highly resistant clones, however, have been obtained in otherwise susceptible progenies of susceptible parents. Selections from two highly resistant sources, *S. andigenum* and *S. demissum*, have been obtained with extremely high field resistance; however, these are too late and need improvement in this characteristic.

Studies relating to the nature of field resistance and methods of measuring such resistance have indicated that i) differences in resistance to penetration by the late blight fungus could not be associated with thickness of cuticle and outer epidermal walls, ii) races of late blight differed considerably in their rate of spread in the field, iii) peroxidase activity as a measure of field resistance was not satisfactory as a screening tool due to effects of environmental factors, and iv) materials grown in greenhouse and field may differ greatly in apparent resistance.

Virus Y:

Two sources of resistance, *S. tuberosum* and *S. stoloniferum*, were included in a program to develop parents with improved resistance to virus Y. The resistance found in *S. tuberosum* appears to be of a generalized type conditioned by multiple factors conferring field resistance. A comparison of progenies derived from varying degrees of inbreeding suggest that genes for field resistance to virus Y can be concentrated by inbreeding. Inbred

progenies exhibited the highest degree of resistance, backcross progenies somewhat less resistance, and outcrossed progenies the least resistance. The resistance available in *S. stoloniferum*, an extremely unadapted species, has also been introduced into *S. tuberosum*. Graft and inoculation tests indicate that immunity and hypersensitivity to virus Y occur in this species.

Several related studies were undertaken to improve testing procedures for virus Y resistance. (i) Greater precision in testing could be achieved through use of screened cages rather than the open field due to greater control over environmental conditions and exclusion of all insect vectors except the desired vector, *Myzus persicae* Sulz. However, ratios for virus Y resistance in segregating progenies showed a high positive correlation between stocks grown in screened cages and those grown in the open. (ii) A group of virus Y isolates were found whose reactions were sufficiently consistent to be of considerable value for screening. (iii) The effect of nutrition on virus Y symptom expression was studied. Plants deficient in potassium developed symptoms more readily than those deficient in other elements.

Heat and drought:

S. tuberosum was used in a program to develop improved parents for heat and drought resistance. Tests were made in the greenhouse using standard heat machine procedures. High positive correlations were obtained between progenies propagated from true seed and subsequent progenies from tubers indicating a high degree of reliability for seedling data and the testing method itself. Results obtained from tests of selfed, intercrossed and outcrossed progenies suggested dominant and additive gene effects for susceptibility to heat and drought. Evidence suggesting cytoplasmic effects for resistance in seedling progenies was not substantiated in tests of subsequent first clonal generation progenies.

Resistance of individual segregates was found to be correlated with plant height and estimated leaf size. Resistance increased as leaf size increased and plant height decreased. These results indicate a close relationship between resistance to heat and/or heat induced drought and factors influencing general plant vigor. This also suggests the possibility of using a "selection index" based on multiple-regression data as an aid in the development of heat and drought resistant parents.

In a related study to improve testing techniques, the relation of heat resistance and chlorophyll stability was investigated. Chlorophyll stability was found to be correlated with resistance of progenies or clones in heat machine tests. This offers a possible rapid, micro-method for evaluating resistance in parent clones and progenies.

Related studies:

An extensive study was conducted to identify tester stocks for yielding ability, specific gravity and tuber type. Specific combining ability effects were large and tended to obscure general combining ability effects. Due to the large specific combining ability effects, it was estimated that a minimum of six test progenies would be necessary to adequately estimate general combining ability for these characters.

Two sources of resistance, *S. tuberosum* and *S. acaule*, were studied in a program to develop parents improved for virus X immunity. Segre-

gation ratios for immunity and susceptibility based on greenhouse tests of seedling plants were obtained for intercrossed and first and second generation selfed progenies. A majority of seedling plants fell into two groups, either susceptible or immune, with a small portion showing atypical symptoms. Retesting of virus X immune plants confirmed initial classifications. Ten clones were found whose selfed progenies were completely immune.

A study was made on the recovery of recurrent parent characters from crosses of *S. demissum* (6n) x *S. tuberosum* (4n) in successive backcross generations using *S. tuberosum* as the recurrent parent. The characters of the recurrent parents were essentially recovered by the third backcross generation.

To obtain information on numerous possible methods of utilizing inbreeding and outcrossing in formulating logical methods for the improvement of parents, an effort has been made to develop horticulturally acceptable, highly inbred clones. Retention of pollen fertility and vigor are serious obstacles. In some lines, it was observed that pollen fertility is reduced very rapidly and completely lost by the second selfed generation. However, one line has been carried to the sixth selfed generation. Second generation selfed clones have been obtained possessing resistance to either virus X, virus Y or heat and drought. Third generation selfed clones are available with resistance to common scab and others with field resistance to late blight.

Haploid stock of *S. tuberosum* obtained from the cooperative Federal-Wisconsin station project have been introduced into the parent improvement programs. Preliminary data on these materials have been obtained for most of the important characters sought in the NC-35 project.

SUMMARY

The NC-35 project has established a unified program designed to develop parents improved genetically for certain important economic characters. Researches have been conducted emphasizing concentration of genes conditioning desired characters, inheritance studies, incorporation of desired characters from IR-1 stocks, and improvement of breeding and testing methods. Though the work is difficult, progress has been made. Twenty-three publications have been reported resulting from researches relating directly or indirectly to the NC-35 project. It is anticipated that more rapid progress will be realized as the use of haploid and other new materials develop.

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