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Potato Breeding Methods

III. A Suggested Procedure for Potato Breeding

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Introduction

Except for a brief period between 1850 and 1890 there was no widespread improvement in potato varieties until about 1930. This lack of progress can be ascribed in a large measure to the natural self nonfruitfulness of cultivated varieties which presented a serious obstacle to sexual breeding work. The initiation of potato breeding work commensurate with the importance of the crop awaited information that would aid in formulating a breeding program, as well as the development of suitable foundation stock. In two previous publications, in 1924 and 1929 (Krantz, *24,* and Krantz and Hutchins, *27*), the author discussed potato breeding methods in the light of information then available. In 1929 a National Potato Breeding Program was formed, the primary object of which was to exchange information and material to facilitate the improvement of potato varieties in the United States. This proved eminently successful as is indicated by the substantial number of varieties introduced to cultivation *(12, 13, 16, 21, 28, 29, 30, 31, 37, 47)*. During this period, information on potato breeding has increased greatly. It seems appropriate at this time to summarize this information and discuss the indicated procedures for potato improvement.

Objectives

The objectives of potato breeding have been to secure improved combinations of such characters as yield, maturity, adaptability to specific locations, market and table quality, and resistance to specific diseases and insects. The characters that influence these economic objectives are extremely numerous in the potato and related tuber-bearing species of *Solanum*. Breeding work is in progress on a large number of these characters as is indicated by the following publications which present the technique practiced in selecting for the various characters *(1, 6, 7, 8, 10, 11, 14, 15, 23, 26, 33, 39, 41, 42, 43, 44, 45, 46, 48, 50)*.

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Tuber characters that are being studied are: shape, smoothness, freedom from knobs and growth cracks, shallow eyes, length of stolons, set and yield, length of rest period, internal composition, dry matter, starch content, cooking quality, mealiness, blackening, hollow heart, hair sprout, resistance to rots initiated by the fungi and bacteria that cause late blight, common scab, wart, fusarium rot, southern bacterial wilt or brown rot, and ring rot, and resistance to infection by plant viruses. The vine characters desired are: early to late maturity, frost and drouth resistance, resistance to injuries caused by flea beetles, leafhoppers, aphids, and psyllids, resistance to numerous virus diseases such as mild, latent, and vein banding mosaics, yellow dwarf, spindle tuber, leafroll as well as resistance to the fungus diseases late blight and early blight.

Type of Inheritance

The cultivated varieties of potatoes of Europe and North America are generally considered as belonging to one polyploid species, *Solanum tuberosum*. In physiological and morphological characters these varieties closely resemble those obtained from Chile, as pointed out by Bukasov *(9)*. Salaman *(41)* presents historical evidence indicating the possibility that *S. andigenum* has entered into the development of European varieties. Both *S. tuberosum* and *S. andigenum* have a somatic chromosome number of 48 *(18, 22, 34, 36, 38, 40, 45, 51)*. They can be readily crossed, and the resulting progeny are as fertile as progeny of intraspecies crosses. The basic chromosome number in the tuber-bearing species of *Solanum* is usually considered as 12, although other numbers have been suggested. Inheritance studies by Lunden *(35)*, Lana *(32)*, and Cadman *(11)* have supplied considerable data which have been explained on the assumption that inheritance is of an autotetraploid type (Haldane, *20*).

Relationship Between Characters

RELATION OF FLOWER, FRUIT, AND TUBER

A rather definite association between fruiting and vegetative plant development has been established by numerous investigators. In general, the reduced vegetative growth associated with fruiting has been explained on the basis of a competition for synthates between the developing fruit and growth of the vegetative structures of the plant. Bartholdi *(4)* studied the effect of flowering and fruiting on the development of underground parts, vines, and tubers. He used a self-fruitful clone and controlled flowering and fruiting as follows:

Treatment 1. The plants were allowed to fruit (fruiting plants).

Treatment 2. The plants were allowed to flower, with flowers removed after collapsing (flowering, nonfruiting plants).

Treatment 3. The flower bud clusters were removed at an early stage (nonflowering, nonfruiting plants).

He then studied the development of underground parts, vines, and tubers of these three types. A summary of some of his results is presented in table 1.

The lowest tuber yield per plant (577 grams) was obtained on plants that were allowed to produce fruits, while the yield per plant where flowers were removed at an early bud stage was 749 grams. Each gram of inflorescence (flower stalk and flowers) excluding fruit caused a reduction in tuber yield of 5.77 grams. Each gram of fruit caused a reduction in tuber yield of 0.48 grams. The 13 grams of inflorescence caused a reduction of 10 per cent, and the 201.4 grams of fruit a reduction of 14 per cent in yield of tubers. Inflorescence and fruit combined caused a reduction in tuber yield of 24 per cent. Calculated for an acre, this reduction is 79 bushels. This inverse association between flowering and fruiting and the tuber yield suggests that selection for high yield would eliminate the liberal flowering and the heavy fruiting types. There is some evidence to support this view in the relatively shy blooming and general self nonfruitfulness of the commonly cultivated varieties. Hence, it would seem that selection for yield would eliminate the undesirable free blooming and the fruiting types, provided shy blooming and self nonfruitful types were present in the population. In order to use the sexual method of breeding it is necessary to retain the flowering and fruiting habit during the process of breeding and eliminate this character when making selections for new clonal varieties. The nature of inheritance of self-fruitfulness makes this relatively easy.

Table 1. Effect of Floral and Fruit Development on Green Weight of Vine and Tubers (from Bartholdi)

Treatment	Average green weight per plant of indicated part			
	Inflorescence	Fruit	Vines	Tubers
		Grams		
1	13.2	201.4	924	577
2	13.0	00.0	1025	674
3	0.0	00.0	1127	749

RELATION OF SHY BLOOM AND STERILE POLLEN TO SELF-NONFRUITING

It has been shown above that a complete absence of floral development would be desirable from the standpoint of tuber production. In breeding, this condition has been approached in the Warba, Red Warba, Mesaba, and Kasota varieties, which will produce a few flowers only under the most favorable conditions. However, most cultivated varieties bloom somewhat more freely, though they are relatively shy bloomers when compared to types present in general seedling populations. Generally, these cultivated varieties are naturally nonfruitful owing to pollen sterility combined with the usual absence of cross pollination.

INHERITANCE OF POLLEN STERILITY

The inheritance of pollen sterility was studied by Fineman *(17)*. He found differential transmission through pollen and egg in reciprocal crosses. The proportion of sterile to fertile pollen plants obtained in five reciprocal crosses between parents of low and high per cent stainable pollen is presented in table 2. It will be noted that the two progenies of a reciprocal cross differ in their proportion of sterile and fertile pollen plants. When the parent having a high per cent stainable pollen was used as a female, a higher proportion of fertile pollen plants was obtained than when the parent with a low per cent of stainable pollen was used as a female. The higher proportion of fertile pollen plants in progenies from high × low than their reciprocal low × high crosses indi-

Table 2. Sterile and Fertile Pollen Plants in Five Reciprocal Crosses of Potatoes (from Fineman)

Parents	Stainable pollen in female parent	Number of plants of progeny in indicated classes: Sterile	Fertile
	Per cent	Number	Number
13-1 × 15-2	25	28	39
15-2 × 13-1	77	5	40
12-7 × 5-29	56	41	10
5-29 × 12-7	72	5	48
17-2 × 11-1	33	30	79
11-1 × 17-2	90	0	151
80-7 × 15-2	56	7	9
15-2 × 80-7	77	0	12
106-55 × 5-2	26	62	50
5-2 × 106-55	75	12	106

cates that some of the factors responsible for sterile pollen plants were eliminated in the pollen and not in the egg. The results indicate an association between the per cent stainable pollen in the female parents and the proportion of sterile to fertile pollen plants in the progeny. This suggests that the factors for complete pollen sterility in sterile pollen plants are the same as the factors for partial pollen sterility in plants that produce both fertile and sterile pollen.

In table 3 is presented the number of sterile and fertile pollen plants obtained from clones selfed and used as female parents in crosses with clones having a relatively high per cent stainable pollen. There is rather wide variation between the selfed and crossed progenies of some clones. In general, a lower proportion of sterile plants was obtained in the selfed than in the crossed progeny except in one or two clones with a high per cent of stainable pollen where there were no sterile pollen plants in the progenies. It will be noted in tables 3 and 4 that the association between the proportion of stainable pollen in the female parent and the proportion of sterile to fertile pollen plants in the crossed and selfed progenies varies widely for different selfs and crosses. This may indicate that elimination of factors for sterility is partial in the pollen, and that amount of elimination varies in different clones.

Table 3. Sterile and Fertile Pollen Plants in Selfed and Crossed Progenies of Potatoes from Seven Fertile Pollen Plants When Used as Female Parents (from Fineman)

Designation of female parents	Stainable pollen	Type of progeny	Number of plants of progeny in indicated classes	
			Sterile pollen	Fertile pollen
	Per cent		Number	Number
13-1	25	Crossed	25	28
		Selfed	6	12
12-7	56	Crossed	41	10
		Selfed	6	11
17-2	33	Crossed	30	79
		Selfed	8	19
80-7	56	Crossed	7	9
		Selfed	6	13
15-2	77	Crossed	5	40
		Selfed	1	43
5-29	72	Crossed	5	48
		Selfed	0	7
11-1	90	Crossed	0	151
		Selfed	0	38

Table 4. Sterile and Fertile Pollen Plants in Nine Related Crosses of Sterile × Fertile Pollen Plants (from Fineman)

Sterile pollen parents	Fertile pollen parents					
	56-1		80-7		15-2	
	Number of plants of progeny in indicated classes					
	Sterile	Fertile	Sterile	Fertile	Sterile	Fertile
	Number					
Cobbler	18	2	23	6	33	13
Triumph	20	4	29	7	12	8
Warba	43	2	19	9	12	3

The inheritance of partial pollen sterility as found in fertile pollen plants has been presented. The following discussion presents the breeding behavior of sterile pollen plants. Table 4 shows the results of crossing each of three sterile pollen varieties with three fertile pollen plants. The Warba crossed with 56-1 gave the highest, and crossed with 80-7 the lowest, proportion of sterile pollen plants obtained in the nine crosses. Crosses in which 56-1 was used as a male parent had in general a higher proportion of sterile pollen plants than 80-7 and 15-2. The presence of both sterile and fertile pollen plants in the nine crosses, with a decided majority consisting of sterile pollen plants, is typical of the breeding behavior of these sterile pollen plants. Segregation into sterile and fertile pollen plants seems to be the rule in crosses of sterile pollen × fertile pollen plants, while crosses between fertile pollen plants may or may not segregate for this character (table 2).

It has been shown that wide variations in the proportion of sterile to fertile plants can be expected between progenies from crosses of sterile by fertile pollen plants and in intracrosses of fertile pollen plants. In general, the proportion of fertile pollen plants is decidedly higher in the latter. The average proportion of sterile to fertile pollen plants obtained in the two types of crosses is given in table 5. In 20 fertile × fertile crosses 71 per cent of the progeny were fertile, compared to 14 per cent in 20 sterile × fertile crosses.

Table 5. Sterile and Fertile Pollen Plants in Hybrid Progenies of Potatoes from Fertile and Sterile Female Parents (from Fineman)

Female parent	Number of crosses	Number of plants of progeny in indicated classes		Fertile pollen plants
		Sterile	Fertile	
		Number	Number	Per cent
Fertile pollen	17	290	629	71
Sterile pollen	20	940	152	14

There are three general types of clones in the potato, indicated by their breeding behavior as female parents: (1) those that produce a high proportion of stainable pollen and give a high proportion of fertile pollen plants in crossed or selfed progenies. In one case where there was 90 per cent stainable pollen, all of the progenies from a selfed and crossed seed were fertile. In two cases where there was 70 per cent stainable pollen, proportion of sterile to fertile pollen plants was about 1 to 8 or 10 in crossed progenies and less in selfed. (2) those that produce about 50 per cent or less of stainable pollen. When crossed, the proportion of sterile to fertile varied from about 4:1 to 1:2. In selfed progenies proportion of sterile to fertile was about 1:2 on the average. (3) those that are sterile that can be used only as females. The proportion of sterile to fertile ranged from 1.5:1 to 21.5:1 in nine crosses where three females were used with three different males; the average of 20 crosses was 6.2:1. By selecting the parents it seems possible to obtain any desired proportion of fertile to sterile, more or less at the will of the breeder.

Ovule abortion is practically absent in the potato. Of hundreds of varieties tested, none with complete ovule abortion has been found *(2, 25, 34)*. Evidence of partial ovule abortion was found by Arnason *(3)* in the Russet Burbank, but it has not entirely prevented the use of this variety as a female parent.

Effect of Selfing

A few studies have been reported on the yield of successive generations of selfing. Krantz and Hutchins *(27)* found a relatively large decrease in tuber yield in the first and second inbred generation as compared to the F_1 generations. Further small decreases were obtained in the third and fourth inbred generations. Guern *(19)* reports that seedlings of the first selfed generations gave yields 20 to 40 per cent below the asexually propagated parent.

The studies reported above by Krantz and Hutchins were continued. The results obtained in five lines by successive generations of selfing are given in table 6.

The yield is expressed in percentage of the F_1 yield for all except line 4 which is expressed in percentage of the I_1 (first inbred generation) yield. The decrease in yield was not large in the I_1 and I_2 in lines 5, 11, 21, and 41. Abrupt decreases were obtained in I_4 with line 5, in the I_3 with line 41, and in the I_2 with line 4.

Table 6. Comparison of Yields in Different Generations of Selfing in Five Lines

Generation	Line 5 Families	Line 5 Yield	Line 11 Families	Line 11 Yield	Line 21 Families	Line 21 Yield	Line 41 Families	Line 41 Yield	Line 4 Families	Line 4 Yield
	Number	Per cent	Number*	Per cent	Number*	Per cent	Number*	Per cent	Number*	Per cent†
I_1	7	92	2	88	5	107	7	76	1	100.0
I_2	8	87	34	70	2	82	22	117	11	48.9
I_3	5	85	......	......	......	......	16	55	15	48.9
I_4	1	64	......	......	......	......	......	......	19	34.8
I_5	1	41	......	......	......	......	......	......	8	31.5
I_6	......	......	......	......	......	......	......	......	4	23.9

* Expressed in per cent of the F_1 yield.
† Expressed in per cent of the I_1 yield.

The average reduction in yield obtained in successive generations of selfing the potato may be indicated by combining the data for all the selfed lines. This comparison for the different generations follows:

Generations (selfed)	*Number of families*	*Yield* *Obtained*	*Yield* *Calculated*
		Per cent	Per cent
1	52	83	59
2	77	82	39
3	36	49	29
4	20	29	24
5	9	27	21
6	4	19	20

The yields obtained in the different generations are given in percentage of the mean F_1 yield from 66 crosses. In the last column is the calculated percentage yield based on the reduction in heterozygosity expected in an amphidiploid.

The yield of the first and second inbred generation lines was 83 and 82 per cent of the F_1. There is a decided drop in the yields of the third and fourth inbred generations. It will be noted that yields obtained were higher than those calculated on the assumption that the yields would be reduced according to the reduction in heterozygosity expected in an amphidiploid. The selection of the parents for the succeeding generation was for other characters than yield. Nevertheless, the individual plant selections probably came from the more vigorous individuals in each family. Furthermore, the weak lines tended to be discarded, for it was only in exceptional cases that a serious effort was made to continue them. The decline in yield in the I_1 and I_2 was not very rapid under the incidental selection for yield that was made during the process of inbreeding.

It has been pointed out that the present evidence favors the view that the potato has an autotetraploid type of inheritance, which according to Haldane *(20)* would result in a slower reduction in heterozygosity than in an amphidiploid.

	F_1	F_2	F_3	F_4	F_5	F_6	F_7	F_{11}
A_2a_2 $7/5\ (5/6)^n - (1/6)^n$	1.00	.94	.805	.6744	.5625	.4685	.3224	.2261
Aa $(1/2)^n$	1.00	.50	.25	.125	.0625	.03125	.0156	.001

The yields obtained in the first, second, and third inbred generations were higher than the calculated yields based on the reduction in heterozygosity in an amphidiploid, but lower than yields calculated on the basis of the reduction in heterozygosity of an autotetraploid. A calculated yield based on the reduction in heterozygosity expected in an amphidiploid is significantly lower than the obtained yield in the I_1, I_2, and I_3, but approaches the obtained yield after the I_3 generation.

The decline in yield of tubers on selfing is accompanied by an increase in the proportion of weak plants that fail to flower. These nonflowering plants are of no value for further improvement work. Hence, selection for desirable combination might well be limited to the F_1 and F_2. If greater homozygosity for the characters in the new combinations is desired, the selections could be selfed one more generation. A more common practice than selfing to secure desirable combinations is the use of less intense forms of inbreeding, such as sib matings, and the use of crosses of individuals having similar characters but different genetic origins. Selfing is also less commonly employed than crossing to determine the breeding behavior of individuals. Nevertheless, selfing is an efficient method for securing new combinations from F_1 selections, for increasing the homozygosity of the desired factors, and for obtaining information on the breeding behavior of selections.

Effect of Crossing

It has been shown that first generation inbred progenies averaged 17 per cent lower in yield than F_1 progenies. The average yields of F_1 progenies obtained from crossing an inbred with an inbred, an F_1, and a variety are given in table 7. A different group of these three types of crosses was tested in each of the four years. It will be noted that no significant difference in yield was obtained between the three types of crosses for the four years. The variations obtained between the tests for different years may be, in part at least, due to the particular parentage of the crosses tested in that year. That some parents combine better than others for

Table 7. Average Yield per Plant Obtained from Different Types of Crosses

Type of cross	1935 Crosses	1935 Yield	1936 Crosses	1936 Yield	1937 Crosses	1937 Yield	1938 Crosses	1938 Yield
	Number	Grams	Number	Grams	Number	Grams	Number	Grams
Single	7	19.3	12	27.6	10	34.6	8	18.1
Three way	15	17.1	13	30.0	19	33.4	4	18.6
Top	6	16.5	13	32.5	6	30.0	31	20.4

yield is commonly known. These results suggest that an inbred selection may be combined with another inbred selection, an F_1 selection, or with a named variety and in all cases good and poor combinations can be expected, depending upon the combining ability of the two parents. The yield of Variety $\times$ F_1 was compared to Variety $\times$ Inbred. The average yield per plant of 26 crosses using F_1 selections was 20.7 grams. In 15 crosses using inbred selections the average yield per plant was 23.4 grams.

The differences between the yields obtained from different types of crosses were small. High yielding selections were obtained from the crosses of variety $\times$ inbred, but none from the inbred $\times$ inbred. The inbreds used as females in the latter cross were self-fruitful. It was further noted that all selections from the inbred $\times$ inbred crosses were self-fruitful. This may account for the failure to obtain high yielding selections from this type of cross.

Breeding Procedure

Certain characteristics of the potato that seem to have an influence on the method of breeding have been discussed. The following summarization of these characters may aid in clarifying the steps in a suggested breeding procedure.

1. The potato is asexually propagated. This makes it possible to select a plant having the greatest heterosis instead of obtaining a cross in which all plants have the necessary heterosis as in seed-propagated crops.
2. Potato varieties and selections are usually heterozygous for most of the characters that differentiate varieties or selections. Wide segregation is obtained in the F_1 progeny of most crosses or in the selfed progenies of clonal varieties.
3. The process of selfing and crossing is simple. Seed in desired amounts can be obtained by controlled pollinations without too much effort.
4. In an experiment where flowering and fruiting were mechanically controlled, there was a close negative correlation between the amount of flower and fruit production and tuber yield. The conclusion is reached that the highest possible

yields may be obtained from varieties that are shy bloomers and that are pollen sterile.

5. Nonfruiting of flowers is usually due to the absence of fertile pollen in this naturally self-pollinated crop.
6. There is less transmission of factors for pollen sterility through the pollen than the egg.
7. The progenies of fertile pollen plants used as female parents consisted of 71 per cent fertile pollen plants as compared to 14 per cent from sterile pollen plants.
8. Fertile pollen plants differing widely in per cent stainable pollen will usually produce a lower proportion of sterile pollen plants in high × low than in low × high crosses.
9. The yield in successive generations of selfing approached a calculated yield based on the reduction in heterozygosity expected in an amphidiploid.
10. F_1 progenies averaged about 17 per cent higher in yield than first generation inbred progenies.

The first three characteristics mentioned tend to simplify or facilitate the usual breeding procedure. The fourth characteristic leads to the conclusion that it is of importance to obtain successive sexual progenies in such a manner that the desired self-sterile plants may be obtained in the progenies. The fifth to the eighth points indicate the general nature of inheritance of sterility and help the breeder plan controlled crosses in such a manner that pollen sterility may be retained in the sexual progenies. The ninth point furnishes the basis for an appreciation of the effects of selfing potatoes. The tenth point emphasizes the average yield of F_1 crosses in comparison with the F_2. To this should be added the importance of using parents with high combining ability, i.e., capability for transmitting factors for yield and other important characters.

A breeding procedure based upon the above-mentioned points may include three major phases: (1) the improvement of fertile pollen plants; (2) the utilization of these fertile pollen plants in crosses to obtain sterile and fertile pollen plants with the characters desired; (3) further crosses between selected sterile and fertile pollen plants of sufficient genetic diversity in origin to give an opportunity to obtain sterile pollen, shy blooming selections of high yielding ability, and an improved combination of other characters. The three phases of improvement are usually not so clearly defined in practice. They usually proceed at the same time and often with the same material. As will be shown later, a system of breeding can be employed that permits improvement in all three phases to be obtained from the same progenies.

SOURCE OF PARENTAL MATERIAL

After determining the objectives of a breeding program, the first step is a selection of the parental material in the light of these objectives. There exists a wealth of material within the species *Solanum tuberosum* L. and among the numerous other wild and cultivated tuber-bearing species of *Solanum,* according to Bukasov *(9)*. The procedure to be followed in selecting the basic parental material will depend on the problems and the extent that a station has experimented with potatoes. It is advantageous in any breeding program to have available a relatively large collection of tested material. In this connection Akeley and Stevenson *(1)* state, "The parental material used in the breeding program has been secured from various parts of the world. The present American varieties are depended upon to contribute high yield, desirable tuber shape, and resistance to three virus diseases, mild mosaic, latent mosaic, and vein banding. Latent mosaic resistance may have come originally from South America. The European varieties have shown high starch content, yellow flesh, and resistance to common scab, late blight, potato wart, and leaf roll. A species immune to late blight and resistant to leafhoppers has been obtained from Mexico. From Russia a number of varieties have been received with a degree of resistance to frost injury." The material in the collections of the United States Department of Agriculture and in the various state experiment stations is freely exchanged through the National Potato Breeding Program.

IMPROVEMENT OF FERTILE POLLEN AND STERILE POLLEN PLANTS

Stuart *(52)* in 1923 recognized the need for better pollen parents. He stated, "The few varieties which do produce ample viable pollen are more or less unsatisfactory from a commercial standpoint, with the result that the seedlings derived from the use of such pollen inherit many of the undesirable characters of their male parent."

The first step in the potato breeding program at Minnesota was to develop pollen plants with as good a combination of commercial characters as the sterile pollen, commonly cultivated varieties. Both crossing and inbreeding were used in the program. Individuals having the desired contrasting characters were crossed. The F_1 selections were then inbred. This inbreeding ranged from selfing the selections to crossing selections having like characters, irrespective of their genetic origin.

The utilization of these fertile pollen plants to obtain sterile and fertile pollen plants with the characters desired can be illustrated by taking a specific example. Breeding work is in progress to obtain an early, scab-resistant commercial variety. The breeding material available is (1) some unadapted scab-resistant European varieties, (2) early maturing adapted varieties, and (3) improved pollen parents.

The varieties with their time of maturity, reaction to scab, and condition of their pollen follow:

European varieties			
Hindenburg	Late	Scab resistant	Partially pollen fertile
Richters Jubel	Late	Scab resistant	Partially pollen fertile
Arnica	Late	Scab resistant	Pollen sterile
American varieties			
Cobbler	Early	Scab susceptible	Pollen sterile
Triumph	Early	Scab susceptible	Pollen sterile
Improved pollen plants			
15-2	Early	Scab susceptible	Highly pollen fertile
80-7-4	Early	Scab susceptible	Highly pollen fertile

The crosses made between late scab-resistant varieties and early scab-susceptible varieties have been separated into three groups, according to the proportion of sterile to fertile plants expected in the progenies.

1. Crosses of Cobbler and Triumph with Hindenburg and Jubel and crosses of Arnica with 15-2 and 80-7-4, using the sterile pollen varieties as female parents.

2. Crosses of Hindenburg and Jubel as female parents with 15-2 and 80-7-4.

3. The reciprocals of crosses in group 2.

The F_1 progenies of crosses in group 1 would be expected to contain a much higher proportion of sterile pollen plants. The ratio obtained in such crosses was 86 per cent sterile pollen and 14 per cent fertile pollen plants. The chances favor the possibility that the best F_1 selections would be sterile pollen plants because of the larger number of sterile than fertile plants in this group. The F_1 progenies of crosses of group 2 would be expected to consist of approximately equal numbers of sterile and fertile pollen plants. The better F_1 selections probably would consist of both sterile and fertile pollen plants. The F_1 progenies of crosses of group 3 would be expected to have very few sterile pollen plants; therefore the chances favor the probability that the best F_1 selections of this group would be fertile pollen plants.

Crosses of group 1 plus either group 2 or 3 would utilize all the material. In this example the crosses were distributed among groups 2 and 3 in a manner that would supply sufficient fertile pollen plants for selection of desired characters without the use of reciprocals.

The proportion of sterile and fertile pollen plants in the F_1 progenies of the various crosses approached the expected. Segregation was obtained for earliness, reaction to scab, and other commercial characters. None of the selections had the exact combination of characters desired. Two of the most promising selections were tested for their adaptability to the potato-growing regions of the state. Their earliness, reaction to scab, and yield as compared to the commonly grown varieties is presented below.

Variety	*Maturity*	*Scab reaction*	*Number of tests*	*Yield per acre*
Cobbler	Early	Susceptible	34	201
Triumph	Early	Susceptible	34	162
43.39-6-40	Early	Medium resistant	34	214
Pontiac	Second early	Susceptible	21	189
Chippewa	Second early	Susceptible	21	192
126.39-1-41	Second early	Medium resistant	21	209

The two selections obtained from crosses of Jubel with 15-2 and Hindenburg with 80-7-4 were adapted to the regions, as indicated by their maturity and yield. A higher resistance to scab was desired.

The next step was to cross the sterile pollen with the fertile pollen selections. One of the crosses made was between the sterile pollen selection 126.39-1-41 and the rare flowering fertile pollen selection 43.39-6-40. To obtain the greatest genetic diversity it seems reasonable to use primarily crosses with no parents in common, although sib crosses could be used also.

The breeder may vary the proportion of sterile to fertile pollen plants in the resultant progenies by a choice of parents and by the direction of the cross as was illustrated for the original crosses. The above crosses should give F_2 segregation for earliness and scab resistance. They would afford an opportunity to secure improvement in all three phases, i.e., early scab-resistant sterile and fertile pollen plants useful for breeding and for cultivation.

Breeding work which entails the use of *Solanum* species other than *tuberosum* may require some modifications from the methods indicated. Salaman *(42)* and Reddick *(39)* have presented in detail their general method of breeding for immunity to late blight, using *Solanum demissum* as the source of immunity. Salaman, after crossing *S. demissum* × *S. tuberosum,* selfed the resulting hybrids for two generations, and then crossed with a variety of *S. tuberosum.* A continuation of selfing and crossing to pollen parents of *S. tuberosum* produced seedlings having blight resistance with good economic quality. Reddick found it difficult to self the F_1 plants of the species cross. This agrees with Becker *(5)* who found the F_1 difficult, if not impossible, to self under controlled pollination. Reddick backcrossed the F_1 plants to pollen parents of *S. tuberosum.* From the third backcross he obtained selections which gave an immune reaction by inoculation and were satisfactory in other characteristics for commercial varieties. The condition of the improved selections in respect to self-fruitfulness is not indicated by the above workers. Crosses at Minnesota between *S. demissum* × *S. tuberosum* gave an F_1 from which no selfed seed under controlled pollination was obtained. Profuse flowering selections set no fruit under cheesecloth cages, but produced an occasional fruit under natural open pollination. Progenies from open-pollinated seed and from F_1 plants backcrossed to *S. tuberosum* tended to be self-fruitful. Immune selections from this first backcross progeny could be used to secure improved immune sterile and fertile pollen plants by the same methods as were indicated for breeding for resistance to common scab. Salaman *(42)* and Reddick *(39)* report no crosses in which the female was the susceptible parent. Stevenson, Schultz, Akeley, and Cash *(49)* were able to transmit resistance to late blight obtained from the W races through the pollen. They state that, "the origin of these races is somewhat obscure as only the immediate pedigrees were received from K. O. Miller (Berlin, Dahlem) with the seed, and these do not indicate the source from which blight resistance was acquired." Sterile pollen plants resistant to late blight have been obtained from crosses using fertile pollen hybrids of *S. demissum* × *S. tuberosum* as females, and partially sterile pollen plants from *S. tuberosum* as males. These sterile pollen plants resistant to late blight can be used as female plants in further crosses for obtaining resistant sterile as well as fertile pollen plants with the desired characters.

The third phase of improvement is the crossing of selected sterile and fertile pollen plants of sufficient genetic diversity in origin to give an opportunity to obtain high yielding selections of sterile pollen and shy blooming plants with an improved combination of characters. It has been mentioned above that such crosses are common in a program of improving sterile and fertile pollen plants. Crosses between the better sterile and fertile pollen plants are continually used during a breeding program to secure improved varieties. Some of the results obtained by such crosses are presented in table 8.

The objective was to secure improved early varieties. The data included in the table on earliness, total yield, and yield of tubers over four ounces give some indication of the improvement obtained. The female parents are shy blooming, sterile pollen varieties or selections with the exception of Jubel which is a partially fertile pollen clone. The improved F_1 selections obtained are shy blooming, sterile pollen plants with the exception of Minnesota No. 42 and 43.39-6-40, which are fertile pollen plants. However, they rarely produce flowers even under conditions favoring profuse blooming. Some of the F_1 selections—Warba, Mesaba, and Kasota—have been introduced as varieties; others—Minnesota No. 42 and 47—are being distributed to the growers at the present time.

Another illustration of how sterile and fertile pollen plants have been employed to obtain improved varieties follows:

Sterile pollen plants, female	*Improved fertile pollen plant, male*	*F_1 selections improved sterile pollen plants*
Charles Downing	Katahdin	Houma
Triumph	Katahdin	Pontiac
Chippewa	Katahdin	Sebago
Green Mountain	Katahdin	Sequoia
Green Mountain	Katahdin	Mohawk
Rural New Yorker	Katahdin	Pawnee
Rural New Yorker	Katahdin	Norkota
Rural New Yorker	Katahdin	Potomac

The above results were obtained in the cooperative breeding work between the United States Department of Agriculture and the various state experiment stations *(13, 16, 21, 37, 47)*. The Katahdin, a fertile pollen clone with general superiority to the commonly cultivated varieties, was crossed on to sterile pollen varieties. The improved F_1 selections, introduced as varieties, are all sterile pollen clones.

The examples given are not intended to cover the methods of breeding that might be employed with success. The choice of methods will be influenced to a large extent by the characteristics of the available material.

The effective use of a breeding method depends to a large extent on the efficiency of selection for the desired combination of characters. Stevenson *(46)* emphasizes the large number of desirable characters in the potato by citing 21 important characters.

Table 8. Use of Sterile and Fertile Pollen Plants in Developing Improved Cultivated Varieties

Parents: Sterile pollen plant	Parents: Superior fertile pollen plant	F_1 selections improved varieties	Early market region: Locations	Early market region: Yield	Late market region: Locations	Late market region: Yield	Red River Valley: Locations	Red River Valley: Yield	Tubers over 4 ounces	
			Number	Bushels	Number	Bushels	Number	Bushels	Per cent	Bushels
		EXTRA EARLY								
Triumph	4-16	Warba	3	210	7	192	16	201	72	145
Selection 9-8	15-2	Minn. 42	3	216	6	208	16	178	86	153
Triumph	15-2-10	35.39-1-40	2	198	3	205	9	187	81	151
		EARLY								
....	....	Cobbler	3	188	7	179	16	195	68	133
Rural	41-1	Mesaba	3	208	7	162	16	178	78	139
Cobbler	13-1	Minn. 47	3	193	6	209	10	191	87	166
Warba	75-5-9	6.39-4-40	3	165	6	214	9	206	83	171
Jubel*	15-2	43.39-6-40	3	208	6	249	11	221	89	197
		MIDSEASON								
....	....	Triumph	3	146	4	191	16	201	81	163
Triumph	29-13	Kasota	2	148	3	270	16	200	7[illegible]	146

* Shy blooming, partially fertile pollen variety.

This is given as a partial list of characters receiving attention by breeders. It directs attention to the need for a well-organized testing program to obtain the desired combination of characters. The following suggested procedure may aid in developing a testing program. In general, the testing procedure in Minnesota has been as follows:

First year: Seed is sown in flats in the fall. It is then transplanted to 3-inch or 4-inch pots and left to grow to maturity in the greenhouse. A bulk sample, consisting of one tuber of each seedling of a family, is harvested.

Second year: The bulk sample of each family is planted in the spring in the field in scab-infected soil at the North Central Branch Experiment Station at Grand Rapids, Minnesota. Individual plant selections are made at harvest.

Third year: The individual plant selections are planted in either 5- or 10-hill rows in the scab test plot. Undesirable selections are discarded on the basis of yield, reaction to scab, and other commercial characters.

Fourth year: The selections are grown in yield tests at two or more of the branch experiment stations and in specialized tests. The tubers may be tested for dry matter, length of rest period, development of tuber rots, and other behavior of tubers in storage.

Fifth and Sixth years: The yield tests are expanded to fields of selected growers in various locations in the state. Each grower's test consists of selections and the common varieties, each grown in 20-hill rows in two randomized blocks.

Seventh year: The yield tests are continued with surplus seed stock of the best selections used for increase plots. The crop from the selections is distributed for trial to members of the Minnesota Potato Improvement Association.

Eighth, Ninth, and Tenth years: The yield tests are continued. If at the end of the ninth or tenth year the selection continues to perform satisfactorily, and the reports from growers of the Improvement Association are favorable, it is named. The Warba variety was named at the end of the sixth year when it was distributed to the growers for trial; the Mesaba and Kasota at the end of the tenth and ninth year, respectively. This year three selections, two at the end of their seventh year and one at the end of its eighth year, are ready for distribution to the growers. It would seem that in a well-organized testing program the selections should be available to the growers for trial at the end of their sixth or seventh year. Since individual plant selections are made in the second year, this allows from four to five years before distribution, and from seven to eight years before naming, to make the various tests which are made concurrently with that of yield. The cooperative tests with the growers are made by the Experiment Station cooperating with the Seed Potato Certification office, and with the Agricultural Extension Division through the extension specialists and the county agricultural agents. Information and publicity concerning the maturity, yield, adaptation, and other characters of a selection after it has been released and named are supplied to the growers by these cooperators.

Summary

The characteristics of the potato that seem to have an influence on the method of breeding are discussed. These include asexual propagation, ease of selfing and crossing, influence of sexual reproduction on tuber yield, the partial elimination of pollen sterility through the pollen, the relation of stainable pollen in female parents to proportion of sterile to fertile pollen plants in sexual progenies, and the effect of selfing and crossing.

Breeding procedures are suggested for the development of better pollen parents, the utilization of these fertile pollen plants in crosses to obtain sterile and fertile pollen plants with the characters desired, and further crosses between selected sterile and fertile pollen plants of sufficient genetic diversity in origin to give an opportunity to obtain sterile pollen, shy blooming selections of high yielding ability with an improved combination of characters.

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