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POTATO BREEDING METHODS II SELECTION IN INBRED LINES[1]

F. A. KRANTZ AND A. E. HUTCHINS

INTRODUCTION

The amount of potato breeding work in progress in America is much less than that of other important food crops. This neglect exists in spite of serious defects in the important commercial potato varieties. The early types will illustrate this condition. Bliss Triumph, owing to its red tuber color and its limited climatic adaptability, is restricted in production to special regions and in consumption to certain markets. Furthermore, great difficulty is experienced in maintaining seed stocks of this variety free from virus diseases. Irish Cobbler has deep eyes with a consequent inconvenience in peeling and waste in utilization; a condition that is a trial to the housewife and should not exist. Early Ohio has a tendency to form knobs and growth cracks when growing conditions vary slightly throughout the season. This frequently results in serious economic losses to the growers. The American grower who desires to produce early potatoes, or who finds quick maturing varieties more desirable for his conditions, is limited to a choice of these three varieties.

Two late maturing varieties, Green Mountain and Rural New Yorker No. 2 and their prototypes, comprise the bulk of the main crop in the United States. They are the best adapted to Minnesota of the late maturing sorts. This fact is attested to by the results of tests in different parts of the state in the last fifteen years, and also by the fact that they have displaced the other late maturing types. These late varieties, however, are not adapted to some of the important potato growing regions of Minnesota, and most of the growers in these regions, particularly in the Red River Valley, are using one of the early varieties for their main crop.

Another indication of the lack of adaptability is the low average yields obtained in comparison with those in other regions in the United States. These low yields are not due to lower soil fertility or to less efficient methods of production. They are due to climatic limitations. The growers have partly offset these low yields by increased efficiency in methods of production, until the cost of production per bushel is lower in Minnesota than in other states. The cost of production per

[1] The potato breeding work here reported was conducted at University Farm, St. Paul, and the Northeast Experiment Station, Duluth, Minnesota. The writers wish to express their appreciation to Superintendent M. J. Thompson of the Northeast station for aid and co-operation during the progress of the work.

acre would not be materially increased by growing an adapted type whose yield would be comparable to that in other regions of the country.

The varieties now grown in Minnesota originated in the eastern part of the United States and were probably selected from among other seedlings because of their greater productivity in that region. It is not surprising that productivity was reduced when they were grown under other environmental conditions. No systematic attempt has been made to produce higher yielding commercial types, altho such improvement seems to be possible. In 1921 work was started to produce a higher yielding commercial variety by applying the principle of "selection in self-fertilized lines" to a vegetatively propagated crop. During the progress of this work approximately 40,000 seedlings have been grown. In the experiments reported here only a small proportion of these have been directly utilized. The material used in the experiments was from various sources and was selected with reference to its suitability to the particular experiment. Indirectly, the entire 40,000 seedlings have contributed to the results reported, as it has been possible to select material adapted for the different studies.

The potato is normally self-pollinated. However, as the varieties are vegetatively propagated by tubers and not by seed, they are in a heterozygous condition similar to that obtained in a normally cross-pollinated crop. Consequently the principle of selection in self-fertilized lines that is applied to normally cross-pollinated crops should also be applicable to the improvement of this crop. This method, in brief, is to inbreed continuously until individuals are secured that breed true for their important characters. This process involves the selection of the best individuals in each generation. These are used as parents for the succeeding generation. When individuals of the desired type that breed true are secured, they are recombined in order to restore hybrid vigor, and from the best recombinations the desired commercial variety is selected. As potato varieties are vegetatively propagated, the characters will remain constant thereafter. It will be noted from this brief outline of the procedure that the problem of potato improvement is essentially one of developing superior individuals for breeding purposes. The usefulness of these individuals will not depend upon their own performance but upon their breeding value as ascertained by a study of their progeny; and upon their ability, when crossed, to produce other individuals of economic value.

The necessity of obtaining such individuals for breeding purposes is due to the character of potato varieties. They are extremely heterozygous and often contain recessive factors for undesirable characters. Furthermore, they frequently exhibit a high degree of sterility, and under certain conditions many varieties have a strong tendency to drop their flowers. Selection in self-fertilized lines offers the best means of eliminating these undesirable features. Furthermore, the potato has characteristics that make it particularly well adapted to this method of breeding. It is normally self-pollinated; artificial crosses can be made easily and quickly; and a single pollination usually gives numerous seeds. The seed retains its viability under good storage for ten or more years; and, finally, clonal propagation of individuals may be continued indefinitely.

NON-FRUITFULNESS IN RELATION TO BREEDING METHODS

A potato plant may be non-fruitful for two reasons: (1) Flowers may drop because of the abscission of the flower pedicel; (2) pollen abortion may be great enough to preclude fertilization. There appears to be no direct causal relationship between the two phenomena. Flowers may drop at any state of development, depending upon the variety and the environment under which it is grown. The difference between varieties in the tendency to drop their flowers has been utilized in varietal classification (Stuart, 14). A large group of seedlings or varieties will usually exhibit a continuous gradation, from individuals that drop their buds at a very early stage to those in which apparently no abscission occurs and in which, if the pollen is aborted, the flowers will adhere to the plant until completely desiccated. The latter extreme is not of common occurrence, for the flowers that persist until fully developed, if not fertilized, will usually fall before drying up. Fertilization usually inhibits any further tendency of the flower to drop. Consequently, an indirect relationship exists between pollen fertility of individuals and the abscission of fully developed flowers.

As previously stated, the character of flower abscission is influenced to a considerable degree by environment. At University Farm, flower abscission is sufficiently prevalent to create a serious problem. In spite of the handicap during the four years, 1921-24, distinct progress was made in obtaining seedlings that would flower at University Farm. Since 1924, the seedlings have been transferred after their first year to the Northeast Experiment Station, at Duluth, to obtain an environment where flower abscission rarely occurs. Under average growing conditions at Duluth, seed is obtained from pollen fertile individuals. The elimination of one of the factors responsible for non-fruitfulness has enabled more rapid progress to be made in overcoming pollen sterility.

The potato is normally self-pollinated, consequently inbreeding would be an easy process if it were not for the high degree of pollen sterility in most varieties. The severity and occurrence of pollen abortion in the cultivated varieties have been ascertained by Stout and Clark (12). Their results show that the major economic varieties approach almost complete pollen sterility. In Minnesota there are six important commercial varieties—Early Ohio, Irish Cobbler, Bliss Triumph, Green Mountain, Rural New Yorker, and Russet Burbank. Two others, Burbank and Spaulding Rose No. 4, are occasionally grown. Green Mountain and Irish Cobbler produce a certain amount of seed under proper environmental conditions. Seed has also been secured from Early Ohio and Triumph, tho seed setting in these two varieties is extremely rare. The other four varieties do not set seed in Minnesota.

The progeny of parents that are scant seed setters usually contain a high percentage of non-seed-producing individuals. Fertile seedlings, however, usually can be obtained in all families if a sufficient number are grown. In certain families the number may be so large that the expense involved would not warrant a continuance of the line. As an instance of this, of 882 seedlings of Irish Cobbler grown in 1925, none set seed. They were replanted from tubers the following year and only 5 produced seed. In the third year, 280 of the original seedlings were again planted but seed was secured from only 8 more, thus making possible selection from only 13 individuals, altho many were grown for three consecutive years. The low percentage of seed production in such families decidedly restricts the amount of selection that can be practiced. Seedlings that do not produce seed in the first three years of their existence are generally discarded for breeding purposes, unless they have other special characteristics of value. Some discarded seedlings might set seed if subjected to a wide range of growing conditions, but the possible results would hardly justify the expense involved.

In order to eliminate the necessity of growing such large numbers and to make possible the use of certain poor seed-producing but otherwise desirable parents, such varieties were crossed with seedlings that set seed liberally. The F_1 from these crosses usually contained enough fertile seedlings for inbreeding purposes. There may be extreme cases of sterility in which a second cross of the F_1 individuals with a seed-bearing parent would be desirable.

Many investigators have studied the nature and cause of sterility in the potato. As the results of their work suggest the possibility of mitigating or circumventing the difficulties that arise through sterility, it may be well to discuss them briefly at this point. The number of chromosomes in the potato has been found by Smith (11), Vilmorin and Simonet (15), Stow (13), and Salaman (9) to be 24. Smith (11) concludes that tetraploidy occurs in the Early Ohio, Early Rose, and

Russet Rural varieties. He suggests that if certain varieties are triploid, as seems to be the case from Lutman's (4) study of Irish Cobbler, Green Mountain, Lookout Mountain, and Early Rose, this might at least partially explain pollen sterility. Stow (13) noted abnormal division of the pollen mother cells, and showed that there was a varietal difference in this respect. He believes "that the abnormal division is neither connected with the hybrid nature of the plant nor the nutritive correlation within its body; but rather due to the environmental conditions or certain special nature of the plant itself." He considers that sterility is mainly the result of abnormal pollen mother cells, which he observed at high temperatures (25° 35°C.). "At lower temperatures (15°-20°C.) on the other hand, the reduction proceeded in a regular manner, producing normal pollen grains." If this interpretation is correct, it may be possible to obtain seed from sterile varieties by experimentally subjecting them to the proper temperatures. This would materially facilitate potato breeding work.

The fact that certain pollen grains abort while others in the same individual survive and are capable of functioning leads to the assumption that pollen grains are differently constituted. This assumption is further supported by results obtained by Salaman and Lesley (10), who have shown by reciprocal crosses that the greater portion, if not all, of the sterility is inherited through the egg. The fact that the eggs will survive conditions that prove lethal to the pollen grains may account to some extent for the widespread prevalence of sterility in cultivated varieties. By the process of inbreeding, sterility would be eliminated through the aborted pollen, and that which was carried over in the egg would be further reduced by elimination of the non-fruiting individuals. These theoretical considerations receive experimental verification from the results of inbreeding. There is a noticeable increase in the number of fertile individuals after the second inbred generation, and lines have been isolated in the third and fourth generations in which a high percentage of individuals are fruitful.

Pollen sterility in the potato makes selection in inbred lines a laborious process. Selection is necessarily restricted to the seed-bearing individuals, and the number of these is frequently limited in the early generations. This necessitates the growing of large populations, only part of which can be utilized. As inbreeding continues, the relative number of fertile individuals increases. Coincidentally other characters have also tended to become homozygous. Consequently the material is less suitable for the selection of the particular combinations desired. This difficulty can be overcome to some extent by crossing desirable sterile types with the best highly fertile types, following by inbreeding and selection in the progeny.

GENERAL EFFECT OF INBREEDING ON THE POTATO

The general effect of inbreeding on the potato is at first to expose to view the heterozygous condition of a potato variety. The variability in the first-generation progeny is very marked. A variety will usually segregate for the easily observable characters that are commonly associated with the individuality of a variety. The variability of this progeny is further emphasized by the appearance of recessive characters. In the second generation some of the lines breed true for certain characters and begin to show individuality. The differentiation into more stable breeding lines is noticeable in the third generation, in which some of the lines assume a distinctive identity while others may still be segregating for important characters.

YIELD OF INBRED LINES

As the lines increase in homozygosity, in general, a loss in vigor occurs. In Tables I and II the relative amount of vine growth and the yields of different inbred generations of two varieties are given. In Table I it will be noticed that the yield is distinctly lower in the second generation than in the first in both 1923 and 1927, when comparative yield tests were made. The yields of the later generations, in which all the lines of each generation are grouped, do not show a significant further decrease.

TABLE I

YIELD OF INBRED LINES DERIVED FROM MINNESOTA ACC. NO. 7416

Year	Generation	No. of lines	Vine growth*	Av. yield, lb.
1923	1	1	4.8	0.39
1923	2	11	4.5	0.28
1925	2	7	4.8	0.35
1925	3	2	4.4	0.38
1927	1	1	3.5	0.84
1927	2	4	2.6	0.42
1927	3	8	4.0	0.43
1927	4	11	3.4	0.31
1928	2	2	6.0	1.49
1928	3	5	6.7	1.07
1928	4	3	6.3	1.76
1928	5	7	6.5	0.84

* Average rating of individuals on a scale of 10.

In Table II the inbred generations of the Early Ohio are compared. The comparative yields obtained in 1927 and in 1928 suggest that very little loss, if any, occurred in this stock after four generations of inbreeding. The yields given in the effect of inbreeding are based on yield of seedlings that survive through the first season. There is frequently a high mortality. The more vigorous seedlings are probably the ones that survive. This tends to raise the average yield of the weaker lines. Furthermore, the vigorous seedlings are more likely to flower and set seed and consequently become the parents of succeeding generations.

TABLE II

YIELD OF INBRED LINES DERIVED FROM EARLY OHIO

Year	Generation	No. of lines	Vine growth	Av. yield, lb.
1927	1	1	4.6	0.82
1927	2	2	4.3	0.62
1927	3	18	5.3	1.03
1928	2	5	8.5	1.86
1928	3	4	8.5	1.88
1928	4	16	6.8	1.37

Data presented in Table III illustrate this condition to some extent. The decline in vigor was different in the four lines derived from the same variety. A more rapid decline in vigor occurred in strains B, C, and D, than in strain A. The table further shows that strain A was easier to maintain than the other three strains. Strains B, C, and D, after the initial decline in yield in the second generation, showed no distinct further drop. Strain A gradually declined in yield and by the fourth generation its yield was approximately the same as that of the other strains.

TABLE III

YIELD AND VINE GROWTH OF FOUR INBRED STRAINS OF MINN. ACC. NO. 7416 SELF-FERTILIZED FOR FOUR GENERATIONS

Year	Inbred Generations	Strain A Vine	Strain A Yield	Strain B Vine	Strain B Yield	Strain C Vine	Strain C Yield	Strain D Vine	Strain D Yield
			lb.		lb.		lb.		lb.
1923	1	4.8	0.39	4.8	0.39	4.8	0.39	4.8	0.39
1923	2	5.8	0.50	4.9	0.32	3.5	0.27	5.2	0.30
1925	2	6.5	0.58	5.3	0.40	...	....	...	....
1925	3	4.6	0.46	...	....	...	....	4.2	0.30
1927	1	3.5	0.84	3.5	0.84	3.5	0.84	3.5	0.84
1927	3	4.2	0.63	...	....	2.5	0.26	2.5	0.28
1927	4	3.4	0.31	3.4	0.31	...	....	...	....

The data presented on the effect of inbreeding on vigor show that there is a general tendency for vigor to be reduced by inbreeding. Owing to elimination of weak seedlings and of lines through failure to set seed, the actual reduction is probably more than the figures indicate. The amount of vigor lost is not so large but that the more vigorous lines can be maintained and utilized.

YIELD OF CROSSES

A study was made to determine the effect of crossing on vigor in the potato, in order to ascertain whether the loss of vigor which accompanies inbreeding could be regained when the best inbred selections were recombined. The method of testing the different combinations varied considerably, depending on the amount of material available. The individual plots usually consisted of 50 seedlings, altho frequently a much higher number was used. The number of plots varied from four systematically distributed plots to single ones.

In Table IV, a comparison is given of the vine growth and yield of fifteen crosses together with that of the progenies of parental varieties. In ten of the eleven crosses for which yield data are available for each parent and the F_1 progeny, the cross-bred individuals gave a higher yield than the mean yield of the two parents. The highest percentage increase obtained over the mean of the parents was 125.7. One F_1 family gave a lower yield than the mean yield of the two parents. If the F_1 progenies are compared with the higher yielding parents in each case, they still show an increase in all but one cross. In this relation the highest percentage increase was 89.2. In this particular cross, two individuals that gave low-yielding progenies produced a relatively high yielding F_1 progeny. An average of the eleven F_1 progenies shows that they outyielded the average mean of the parents by 50.3 per cent, and the average yield of the highest yielding parent by 31.5 per cent.

The differences obtained between the yield of F_1 crosses and that of the progenies of their parents were larger than those obtained between the different inbred generations. This difference in yield may be due to a combination of loss in vigor from selfing the parents and an increase in vigor due to crossing. The yields of three parental families and of their F_1 progenies were compared. This tends to eliminate any decrease in yield that may have occurred because of selfing the parents. The results seem to indicate that the greater part of the difference is due to the beneficial effect of crossing rather than to any detrimental effect of inbreeding.

The data presented in Table V show a decided increase in yield from crossing in two cases and practically no gain in the other case.

The general tendency of the F_1 progenies to be vigorous and high yielding has an important bearing on breeding methods. The data given in Tables IV and V show that progenies derived from either seedlings or varieties are distinctly inferior in yielding ability to the F_1 progenies. In fact, no seed has been obtained from any source that gives progeny yielding as high as the progeny of crossed seed. In observations made on approximately thirty thousand seedlings, few

TABLE IV

COMPARISON OF F_1 CROSSES WITH PROGENIES OF PARENTAL VARIETIES

Year	Cross	Vine growth			Average yield lb.			Inc. in yield over mean of parents per cent	Inc. in yield over highest parent per cent
		♀	♂	F_1	♀	♂	F_1		
1923	Green Mountain × Minn. Acc. No. 7416	5.9	4.8	6.5	0.27	0.39	0.61	84.8	56.4
1923	Irish Cobbler × Lookout Mountain	5.6	5.4	6.1	0.28	0.26	0.53	96.2	89.2
1923	Early Ohio × Minn. Acc. No. 7416	5.8	4.8	5.8	0.49	0.39	0.51	15.9	4.0
1924	Triumph × Minn. Acc. No. 7416	4.0	5.1	5.3	....	....	....	....	....
1924	Irish Cobbler × Minn. Acc. No. 7416	4.6	5.1	4.8	....	....	....	....	....
1925	Irish Cobbler × Peerless	5.0	6.1	5.9	0.37	0.32	0.49	42.0	32.4
1925	Irish Cobbler × Minn. Acc. No 7416	5.0	...	4.6	0.37	....	0.39	....	5.4
1925	Peerless × Lookout Mountain	6.1	...	6.2	0.32	....	0.42	....	31.2
1925	41.22-40-24 × 28.22-8-24	5.5	4.6	6.7	0.36	0.46	0.55	34.1	19.5
1927	Triumph × 12.23-4.1-25	2.5	3.0	3.8	0.65	0.39	0.76	46.1	16.9
1927	Cobbler × 12.23-4.2-25	4.4	3.0	4.3	1.03	0.39	0.61	−16.3	−68.8
1927	Triumph × 41.22-2-25	2.5	4.0	4.4	0.65	0.88	1.17	52.0	32.9
1927	15.22- 1-25 × 41.22-2-25	2.0	4.0	4.0	0.20	0.88	1.15	112.9	30.6
1927	15.22- 1.25 × 4.20-10.4-25	2.0	3.0	4.0	0.20	0.66	0.69	60.4	4.5
1927	12.23-10.25 × 4.20-10.4-25	3.0	3.0	4.6	0.39	0.66	1.21	125.7	83.8
							Average	50.3	31.5

progenies have been found to approach the vigor of crossed seed and none that equaled the vigor of the heaviest yielding F_1 progenies. Consequently it should be far easier to select seedlings from the F_1 progenies that would be higher yielding than the commonly grown varieties than from progenies of any other source.

TABLE V

YIELD OF THE P_1 GENERATION COMPARED WITH THE F_1

Year	Parental families		Vine growth			Average yield, lb.			Inc. yield over mean of parental families per cent	Inc. yield over highest parental family per cent
	♀ P_1	♂ P_1	♀ P_1	♂ P_1	F_1	♀ P_1	♂ P_1	F_1		
1927	42.44 ×	15.22	4.36	2.00	3.74	1.026	0.200	0.63	3.2	−63.4
1927	15.22 ×	4.20	2.00	3.48	4.64	0.200	0.844	1.24	138.4	47.6
1927	41.22 ×	4.20	4.58	3.48	5.60	0.819	0.844	1.42	71.0	69.0

Studies on the vigor and yielding ability of F_2 and later generations show that vigor and yield tend to decline after the F_1 generation. The comparative yield and vine growth for F_1 to F_3 generations of two crosses are given in Table VI. A small reduction in yield occurred in the F_2 generation and a greater in the F_3 generation. In this limited study the decline was greater in the F_3 generation than in the F_2 or the F_4 generation.

TABLE VI

RELATIVE VIGOR OF F_1 TO F_3 GENERATIONS OF TWO CROSSES

Cross	Year	Generation	No. of lines	Vine growth	Av. yield per seedling
					lb.
13.22-18-24 × 28.22-8.24	1927	F_1		6.5*	1.14*
	1927	F_2	5	7.6	1.22
	1927	F_3	2	6.3	0.93
41.22-40.24 × 28.22-8.24	1927	F_1		6.7*	1.10*
	1927	F_2	2	6.4	0.97
	1927	F_3	34	4.9	0.77
	1928	F_3	4	7.5	1.99
	1928	F_4	13	6.9	2.27

* Adjusted on the basis of checks from 1926 data.

The data presented on the effect of inbreeding and cross-breeding indicate a general tendency for vigor to be reduced through inbreeding. This loss is probably greater than the yield data indicate, because of the loss of weak seedlings and the tendency to eliminate weak seedlings and lines through their failure to set seed. Cross-breeding has a tendency to increase the vigor, as is shown by the greater vigor in the F_1 progenies. One may assume, therefore, that crossing desirable inbred lines results in vigor equaling or surpassing that of the original parents.

Selection in Inbred Lines

The physical limitations on the number of lines that can be grown makes it obligatory to practice some type of selection so the desirable germ plasm can be sorted out and saved and the undesirable discarded. Most of the desirable morphological characters have been segregated by selecting individuals possessing them and by testing the correctness of the observations through a study of the progeny in later generations. The isolation of these characters appears to be progressing so well that no special studies have been deemed necessary to determine a more accurate basis for the selection. Some of the plant characters isolated on the basis of field records and observations are differences in color and form, second growth, growth cracks, depth of eye, smoothness and russeting of tubers, length of stolons, number of stolons, number of tubers per stolon, number and size of tubers per plant, habits of vine growth, and other vine characters. Two other characters, yield and time of maturity, were studied to determine on what basis selection for them could be made most effectively.

BREEDING BEHAVIOR OF EARLY AND LATE VARIETIES

To determine the relationship between the time of maturity of plants and the breeding behavior of their progeny, a study was made of the progenies of commercial varieties whose relative time of maturity is well known. These varieties fall naturally into two classes.

Early maturing: Bliss Triumph, Irish Cobbler, Early Ohio

Late maturing: Green Mountain, Rural (smooth and russet), Red McCormick (Lookout Mountain)

Altho the varieties within these groups vary, the groups are fairly well defined. As the phenotypic behavior has been well established by observations of commercial plantings throughout the country, a study of their genotypes should be of interest. The breeding behavior of these varieties was determined from a study of their progeny and from the progeny derived from crosses in which they appear as parents.

By reference to Table VII it may be seen that the maturity of the seedlings corresponded rather closely to that of the parents. In 1923, the progenies of Early Ohio and Lookout Mountain were compared. The Early Ohio had matured 54 per cent of its progeny on September 10; the Lookout Mountain, 8 per cent. In 1924 a study was made of the progenies of the Triumph and Cobbler varieties. The Triumph had matured 77 per cent of its seedlings by September 10; the Cobbler, 54 per cent. In 1927 a comparison was made of the relative time of maturity of the progeny of Triumph, Cobbler, Early Ohio, and Green Mountain. The percentage matured by September 10 in the four varieties was 73, 63, 50, and 10, respectively. On the basis of time of maturity of offspring, the five varieties may now be listed in the following order: Bliss Triumph, Irish Cobbler, Early Ohio, Green Mountain, and Red McCormick.

TABLE VII

BREEDING BEHAVIOR OF FIVE COMMERCIAL VARIETIES AS INDICATED BY THE COMPARISON OF THEIR SEEDLING PROGENY IN RELATION TO THE NORMAL PERIOD OF MATURITY

Variety	Year	Condition of seedlings on September 10			
		Number			Percentage mature
		Mature	Immature	Total	
Early Ohio	1923	120	101	221	54
Red McCormick	1923	3	34	37	8
Triumph	1924	108	32	140	77
Cobbler	1924	6	5	11	54
Triumph	1927	63	23	86	73
Cobbler	1927	26	15	41	63
Early Ohio	1927	13	13	26	50
Green Mountain	1927	5	47	52	10

A comparison of the behavior of the varieties in crosses with a common pollen parent further confirms the results from the study of progenies obtained by self-pollination. Six groups of such crosses are shown in Table VIII. Triumph, Cobbler, and Early Ohio retain their relative ranking when crossed with a medium early parent, Minn. Acc. No. 7416. The percentage of F_1 progeny mature on September 10, 1923, was 86, 77, and 50, respectively. A similar test of Triumph and Cobbler in 1924 gave respectively 62 and 52 per cent of mature seedlings on September 10. In the four succeeding groups of crosses, the progeny of Russet Rural is compared with that of Triumph, Cobbler, and Green Mountain. In Group III, Triumph and Russet Rural are crossed with a very late maturing parent, 4.20-1-24. The percentage of the F_1 progenies mature on September 10, was 24 and 19, respectively. When these varieties were crossed with a medium late maturing seedling, 41.22-1-25, the F_1 progenies matured 35 and 6 per cent of their respective seedlings by September 10. In Group V, Cobbler and Russet Rural are crossed with a late maturing seedling, 11.24-1-25. In the F_1 progenies of these crosses the percentage of mature seedlings was 39 and 20, respectively. In Group VI, where two late varieties, Green Mountain and Russett Rural, were crossed with a late maturing seedling, 11.24-3-25, the F_1 progeny of the Russet Rural cross matured 9 per cent more of its seedlings by September 10 than did the progeny of the Green Mountain cross. The results of these crosses tend to confirm the previous ranking of Triumph, Cobbler, Early Ohio, and Green Mountain based on the behavior of progeny of self-pollinated seed. Russet Rural appears from the data obtained in these crosses to be genetically slightly earlier than Green Mountain.

From the data presented in Tables VII and VIII, some general deductions seem to be justified. The early maturing varieties—Triumph, Cobbler, and Early Ohio—give distinctly earlier maturing progeny than the late varieties—Rural, Green Mountain, and Red McCormick. The difference between the time of maturity of the seedling progeny of the early maturing varieties is greater than between the individual varieties when these varieties are asexually propagated. The value of a seedling or a variety in respect to the character of maturity can be more quickly and accurately ascertained by studying its breeding behavior in comparative tests than from its phenotypic behavior.

TABLE VIII

FACTORS FOR MATURITY OF SIX COMMERCIAL VARIETIES AS INDICATED BY THEIR BEHAVIOR IN CROSSES

Group	Parents	Year	Condition of seedlings on September 10			
			No. of seedlings			Percentage
			Mature	Immature	Total	mature
I	Triumph × Minn. Acc. 7416	1923	42	7	49	86
	Cobbler × Minn. Acc. 7416	1923	40	12	52	77
	Early Ohio × Minn. Acc. 7416	1923	30	30	60	50
II	Triumph × Minn. Acc. 7416	1924	54	33	87	62
	Cobbler × Minn. Acc. 7416	1924	43	39	82	52
III	Triumph × 4.20-1-24	1927	22	70	92	24
	Russet Rural × 4.20-1-24	1927	7	29	36	19
IV	Triumph × 41.22-1-25	1927	11	20	31	35
	Russet Rural × 41.22-1-25	1927	2	29	31	6
V	Cobbler × 11.24-4-25	1927	12	19	31	39
	Russet Rural × 11.24-4-25	1927	7	28	35	20
VI	Green Mountain × 11.24-3-25	1927	6	27	33	18
	Russet Rural × 11.24-3-25	1927	9	24	33	27

INHERITANCE OF TIME OF MATURITY

An analysis of the data on a strict genetic basis can not be made. The data are, however, suggestive of several points. Müller (5) studied the genetic characteristics of potato varieties of different maturity. His results show that the later the average maturity the greater is the negative skewness of the frequency curve; the earlier the average maturity of a family the greater is the variability as measured by the standard deviation; the means of the crosses lie between the means of the progeny of the self-pollinated parents. Müller attempts to explain these results on the basis that late maturity is dominant and that multiple factors are involved. He points out that the increased variability of the early families does not harmonize with the supposition that late maturity is dominant. He suggests that this discrepancy might be accounted for by the shorter period of daylight and dropping of temperature as the season progresses, thus prolonging the life of individuals and placing them in later classes than their genotype would warrant. It appears, however, that the results could be more easily explained if it were assumed that earliness was dominant and that multiple factors were involved. Müller was working with medium early varieties that would probably be heterozygous for this character. This would account for their greater variability as compared to the progenies of the late maturing varieties; the latter, having more homozygous recessive factors, would tend to breed true.

TABLE IX

COMPARISON OF TIME OF MATURITY OF PROGENY OF COMMERCIAL VARIETIES AND THEIR F_1 VARIETAL CROSSES

No.	Parents	Maturity of parents	Year	Condition of seedlings on September 10			
				Number of seedlings			Percentage
				Mature	Immature	Total	mature
I	Triumph	Early	1924	108	32	140	77
	Triumph × Minn. Acc. No. 7416			54	33	87	62
	Minn. Acc. No. 7416	Medium		15	56	71	21
II	Cobbler	Early	1924	6	5	11	54
	Cobbler × Minn. Acc. No. 7416			43	39	82	52
	Minn. Acc. No. 7416	Medium		15	56	71	21
III	Early Ohio	Early	1923	120	101	221	54
	Early Ohio × Minn. Acc. No. 7416			30	30	60	50
	Minn. Acc. No. 7416	Medium		17	22	39	44
IV	Triumph	Early	1927	63	23	86	73
	Triumph × 41.22-2-25			12	5	17	71
	41.22-2-25	Late		7	13	20	35
V	Cobbler	Early	1923	6	2	8	63
	Cobbler × Red McCormick			36	27	63	57
	Red McCormick	Late		3	34	37	8
VI	Triumph	Early	1927	63	23	86	73
	Triumph × No. 12.23			30	39	69	43
	No. 12.23	Late		33	59	92	36
VII	Green Mountain	Late	1927	5	47	52	10
	Green Mountain × 11.24-3-25			6	27	33	18
	11.24-3-25	Late		..	..	..	..

In studies made at University Farm in which the behavior of crosses was compared with that of seedling progenies of the same parents, earliness tended to behave as a dominant character. The data are presented in Table IX. It will be noted that in crosses I, II, and III, in which the early varieties were crossed with a medium maturing parent, the F_1 seedlings approached more closely in behavior the progeny of the early parent. The data from these three crosses further show a relationship between the earliness of the early parent progeny and of the F_1 seedlings. In crosses IV, V, and VI, early varieties were crossed with late varieties. In two of these crosses, IV and V, earliness behaved as a dominant character; the percentage of seedlings that matured by September 10 nearly equaled the percentage that matured in the progeny of the early parent. In cross VI, the F_1 progeny behaved more like the seedlings of the late parent. In cross VII, in which two late parents were crossed, the F_1 seedlings were late. In the crosses reported by Müller (5) the F_1 progeny clearly tended to be intermediate between the two parents. Since varieties classed as second earliest were used, they were probably later maturing than Bliss Triumph and Irish Cobbler, which would explain the difference in the results obtained.

SELECTION FOR EARLY MATURITY

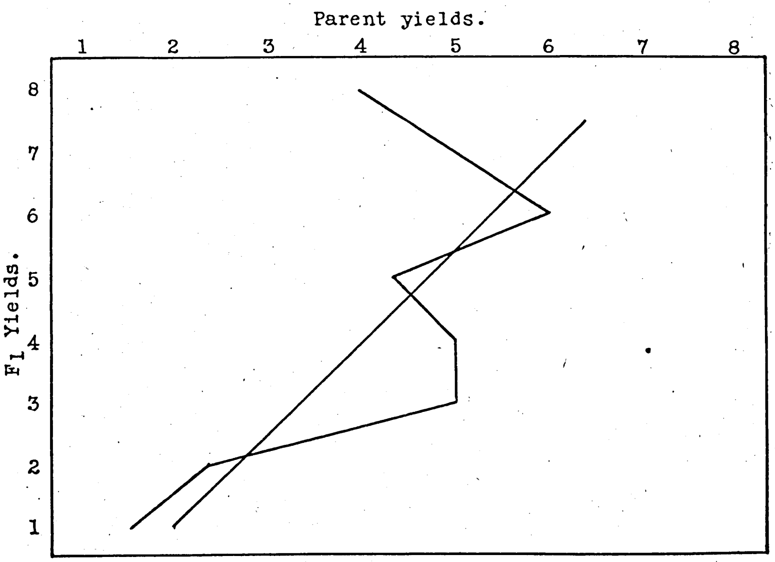
It is interesting to note that the earliest varieties obtainable in the United States, i.e., Bliss Triumph, Irish Cobbler, and Early Ohio, did not breed true for earliness. As these varieties are heterozygous for at least some of the factors that produce earliness, it should be possible to obtain seedlings from their progenies that were more homozygous and consequently earlier maturing than the parent varieties. While selection of the earlier maturing seedlings can be started to advantage in their first and second years, it is not until the third season, because of a tendency to delay maturity, that an accurate comparison with the parent variety can be made. Delayed maturity of the seedlings appears to be associated with the amount of reserve nutrients available when the plants are started. As the size of the tubers available for planting from individual seedlings the second year may vary, some error is involved in making the selections on maturity at this time. A comparison with the parent variety of 229 Irish Cobbler seedlings in their third season indicates that both earlier and later maturing seedlings were obtained. The comparison showed 98 seedlings to be earlier than, 91 similar, and 40 later than the parent. If such progenies were fruitful it would be easy to obtain individuals that would breed true for earliness. But the progenies from early varieties have been highly unfruitful.

In order to obtain early seedlings with viable pollen, crosses of fertile seedlings and early seedlings of varieties were made. This was done because of the difficulty of obtaining early lines from late parents, which, owing to their high fertility, were the best sources of inbred lines. More recently some early lines have been isolated from early varieties. This method of crossing followed by inbreeding, and then repeating the process if necessary, appears to be a satisfactory one for obtaining early seedlings that have viable pollen and the other characteristics desired. A comparison of the progeny of the 34 earliest seedlings with the progeny of Triumph, Cobbler, and Early Ohio shows that 6 seedlings from their breeding behavior appear to be genetically as early as the Triumph variety; 20 seedlings are genetically earlier than the Cobbler or as early; while all of the 34 seedlings are genetically as early as the Early Ohio or earlier. All these seedlings, judging from their ability to set seed, have sufficient viable pollen to function as pollen parents. A comparison, in 1927, of 172 families, including self and F_1 families derived from certain commercial varieties, shows that there were 8 seedling families as early as the Triumph family; 24 families as early as the Cobbler family or earlier; 74 families as early as the Early Ohio family or earlier; 147 families as early as the Green Mountain family or earlier. Twenty families of the 172 in the test were as late as the Red McCormick family or later. The individuals of all the families in the latter class were still green when they were killed by frost, consequently their relative rank could not be ascertained. The number of seedlings of each family is too small to allow a definite conclusion to be drawn as to the relative earliness of any particular family. They show as a group, however, that definite progress is being made toward the production of breeding material that has the combination of earliness and fertility.

The studies on maturity may be briefly summarized. The breeding behavior of standard commercial varieties when self-pollinated and when crossed show that where wide differences in maturity exist a distinct difference will also be found between the genotypes of these varieties or individuals. The Triumph, Cobbler, and Early Ohio varieties, which mature at relatively the same time, show distinct differences in their genetic constitution in regard to maturity. Therefore, in selecting for earliness, late maturing seedlings can be safely discarded, while the early maturing seedlings should be further sorted out on the basis of breeding behavior. The breeding behavior of early maturity as a character appears to be typical of characters whose expression is dependent on dominant multiple factors. The method used to obtain early breeding stock was to cross selected fertile seedlings and early seedlings or varieties, and again select in the inbred lines obtained from the F_1 progeny. This process can be repeated, using the earliest lines obtained, until the lines are as early as the earliest seedlings or varieties obtainable. Seedling lines have been obtained by this method that compare favorably in early maturity with the progeny of the early varieties and, in addition, have the fertility required in breeding stock.

PRODUCTION OF HIGH YIELDING SEEDLINGS

It has been shown in Tables I to VI that there is a tendency for the yield to decrease during the process of inbreeding, and that this loss in yield is regained and frequently increased by appropriate crossing. All crosses do not yield equally well, hence it is important to know what relation, if any, exists between the yields of parents and their corresponding crosses. A few studies have been made of corn, bearing on the relation between the inbred strains and the F_1 crosses. Kisselbach (2) found that high yielding corn strains have, as a rule, given better yielding F_1 crosses than low yielding strains. Richey (7) and Richey and Mayer (8) found no such general relation. More recently Nilsson-Leissner (6) and Jorgenson and Brewbaker (1) obtained results which led them to conclude that selection of the most vigorous selfed lines is desirable in corn, but that the only method of learning the better F_1 combinations is by actual trial.



In 1927, the yields of 47 F_1 potato crosses were obtained. Owing to soil variability at the Northeast station, where all the parents were grown, the yields of these parents were not sufficiently accurate to justify their use. Both parents of 18 of these F_1 crosses were also grown at University Farm. The regression of parent yields on yield of F_1 is shown in Figure 1. The correlation coefficient is 0.5564 ± 0.1079.

This shows a distinct correlation between the mean yield of the parents and their F_1 progeny. The number of crosses involved was small. The parents were very heterogenous as to origin; and it is possible that the high yielding parents were better adapted to growing conditions at University Farm, consequently their F_1 progeny were also better adapted. The results suggest the desirability of further studies to determine if such a general relationship can be expected. Even if such a general relationship exists, there would be little reason for discarding the poorer yielding lines before determining by actual trial their value in recombinations.

A comparison of the yield of F_1 crosses with that of inbred lines and seedling families of standard varieties indicates that a high yield can probably be obtained by recombining the inbred lines even if no selection is made for this character. In 1927, seedling families were grown from Triumph, Cobbler, Early Ohio, and Green Mountain varieties. The lowest yielding family was obtained from the Triumph variety with 52 bushels per acre. The Green Mountain family gave the highest yield, 103 bushels per acre. Of the 57 inbred lines in the test 9, or 15.8 per cent, gave a higher yield than the Green Mountain family, and 25, or 43.9 per cent, gave a lower yield than the Triumph family. Of the 47 F_1 crosses in the test 25, or 53.2 per cent, gave a higher yield than the Green Mountain family and only 3, or 6.4 per cent, gave a lower yield than the Triumph family. It is of interest to note that, in the absence of selection, more than 50 per cent of the F_1 crosses gave a higher yield than the highest yielding seedling progeny of four standard varieties. The superior yielding ability of these F_1 crosses can be illustrated in another manner. The average yield of the 57 inbred lines was 58 bushels per acre; of the seedling families of the four standard varieties 75.5 bushels per acre; and of the 47 F_1 crosses 93.2 bushels per acre.

DISCUSSION

In a previous publication (Krantz, 3) it was pointed out that the employment of the method of "selection in self-fertilized lines" was particularly appropriate in a vegetatively propagated crop such as the potato. The studies presented in this paper have been concerned with the soundness of the general principle in its specific application to the improvement of the potato, and in establishing economical and effective methods for its application.

The object of selection in self-fertilized lines of potatoes is to secure fertile breeding stock that breeds true for the important economic characters, and from which abnormalities and other undesirable characters have been eliminated. The problem is essentially one of developing superior individuals for breeding purposes. The value of these individuals will not depend upon their own performance but upon their breeding behavior as ascertained by a study of their progeny and upon their ability when crossed with each other to produce individuals of economic value.

The procedure followed in producing these individuals is both analytical and synthetic. The desirable features of our commercial varieties must be separated from the undesirable; then by a building-up process individuals of the desirable types must be constructed. Inbreeding is the genetic method of analysis. It exposes characters and shows in what degree of purity these characters exist within the individual, thus enabling a selective process to separate the desirable elements into pure line groups. By crossing, these groups may then be split up and recombined to meet specific requirements. The above process is a method by which a concrete objective may be attained; at the same time it lays the foundation for a subsequent higher objective. The process of constructing breeding material and the introduction of improved combinations of characters to replace economic varieties will necessarily progress simultaneously, as the latter must be used in measuring the progress made toward the first objective. Perfection in breeding stock and in varieties may be an infinite aim. This, however, is immaterial as long as progress in the improvement of breeding stock is reflected in the production of better varieties.

SUMMARY AND CONCLUSIONS

1. The prevalence of non-fruitfulness in the potato is primarily responsible for the paucity of potato breeding work. The non-fruitfulness due to flower dropping has been eliminated by transferring the seedlings after their first year to a more favorable environment. The failure to set fruit because of pollen abortion has been overcome by inbreeding partially fertile varieties and by crossing sterile and weak pollen-producing varieties with fertile seedlings and then inbreeding the F_1 generation. Pollen sterility is eliminated from these future generations through its lethal effect on the pollen grains that carry it and through the elimination of the non-fruiting individuals of the progeny. Because the eggs are not affected, and consequently transmit the sterility to succeeding generations, the process of elimination is slower than it otherwise would be. The increase in fertility is, however, marked after the second and third inbred generations.

2. The effect of inbreeding on commercial varieties of the potato is, first to expose their heterozygous condition. After the first generation an appreciable reduction in variability is noted. In the third and fourth generations, lines begin to show sufficient uniformity that their individuality can be recognized.

3. A reduction in vigor accompanies the approach of the lines to homozygosity, as is indicated by smaller vine growth and decreased

yields. The reduction in yield for the two varieties in which lines have been inbred for four or more generations has been approximately 40 per cent below the yield of the first inbred generation. The results obtained from crosses between varieties and between inbred seedlings show that the loss in yield occasioned by inbreeding can be regained and in many cases reduced by appropriate recombinations. Two crosses between inbred lines have been carried to the F_3 generations. The difference in yield between the F_2 and the F_3 generations is approximately equal to that between the first and second inbred generations of a variety.

4. Most of the important economic characters are fairly easy to fix in the inbred lines. The process is one of discarding the poorer seedlings and lines. However, early maturity as a genetic character has been found difficult to isolate. Results from selfed and crossed progenies suggest that its expression is dependent upon dominant multiple factors. A study of the seedling progenies of standard varieties shows distinct differences between the progeny of Bliss Triumph, Irish Cobbler, and Early Ohio. The varieties studied may be ranked according to the earliness of their seedlings as follows: Bliss Triumph, Irish Cobbler, Early Ohio, Green Mountain, and Lookout Mountain. Rural New Yorker, from its behavior in crosses, appears to be genetically slightly earlier than Green Mountain.

The genetic data obtained from self-pollinating and crossing of standard varieties enable the following conclusions to be drawn: Where a wide difference in maturity exists between varieties, such as between early and late maturing ones, their seedling progenies will show the same relative difference. However, varieties of relatively the same period of maturity such as Triumph, Cobbler, and Early Ohio, may show distinct differences in their genetic constitution in regard to earliness. It would be desirable, therefore, in selecting for early maturity, to select first on the basis of individual behavior, and second on the ability to transmit this character to its seedlings. A handicap in making selections on this basis results from the high degree of sterility found in the progenies of the early varieties. A method consisting of crossing the earliest available fertile seedlings with the early varieties and selecting from later generations derived from these crosses has enabled the isolation of lines in which earliness equal to that of the progeny from the early varieties is combined with relatively high fertility. Doubtless lines homozygous for earliness can be isolated from this material.

5. A study was made to determine the importance of yield as a character to be considered when selecting inbred lines. A comparison in 1927 of the yield of 18 F_1 crosses with the yield of the parents gave a correlation coefficient of 0.556 ± 0.108. This suggests the

possibility of an important relationship. A comparison of the yield of F_1 crosses with the yield of inbred lines and seedling families of the Triumph, Cobbler, Early Ohio, and Green Mountain varieties indicates that a high yield can probably be obtained upon recombining the inbred lines even if no selection for high yield is practiced in them. The average yield of 57 inbred lines was 58 bushels per acre; of the seedling families of the four standard varieties, 75.5 bushels per acre; and of the 47 F_1 crosses made from lines picked at random, 93.2 bushels per acre. The most economical procedure appears to be to determine by actual trial the best recombinations and to select the best individuals from the highest yielding recombinations for a comparative test with the standard varieties to determine which individuals would be of value in commercial production.

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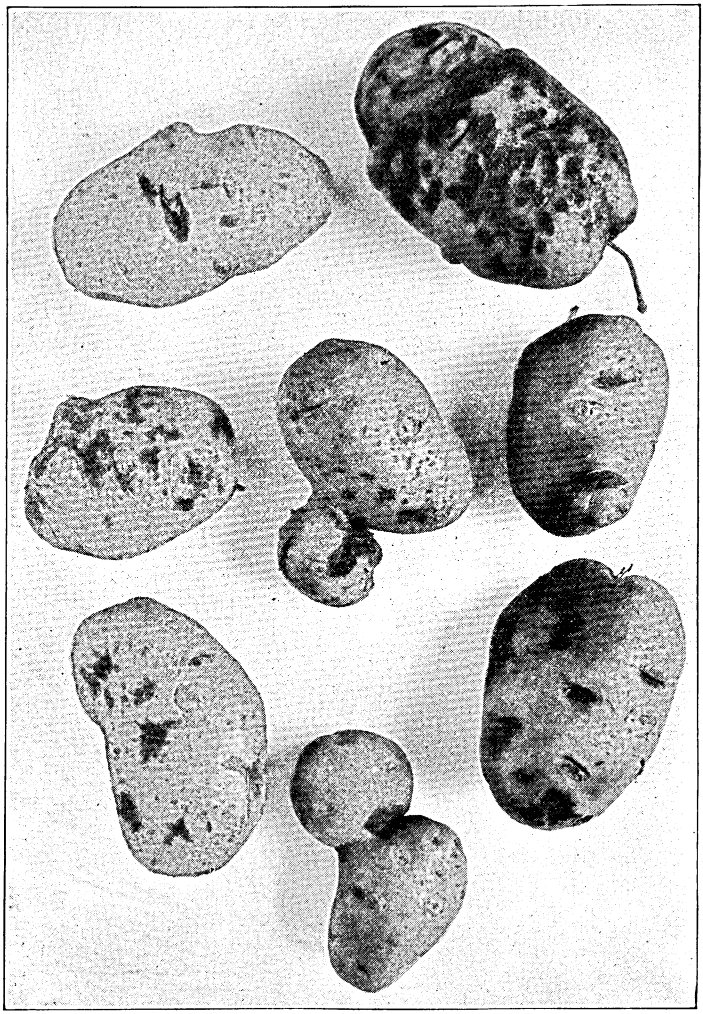

Plate 1. Tendency of Early Ohio Potatoes to Form Knobs

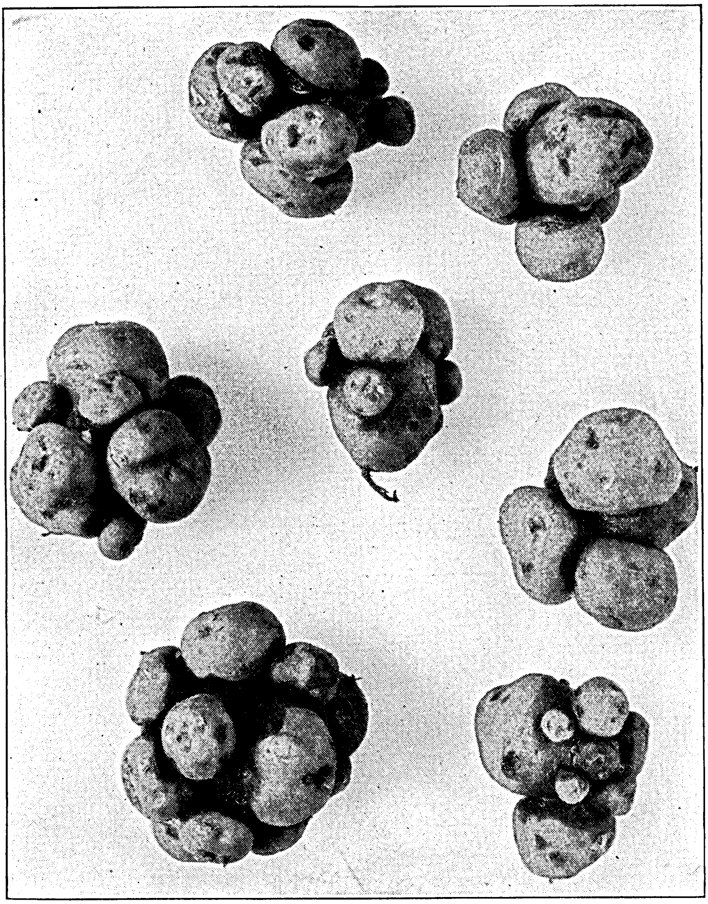

Plate 2. Early Ohio Seedling Showing Extreme Tendency Toward Development of Knobs

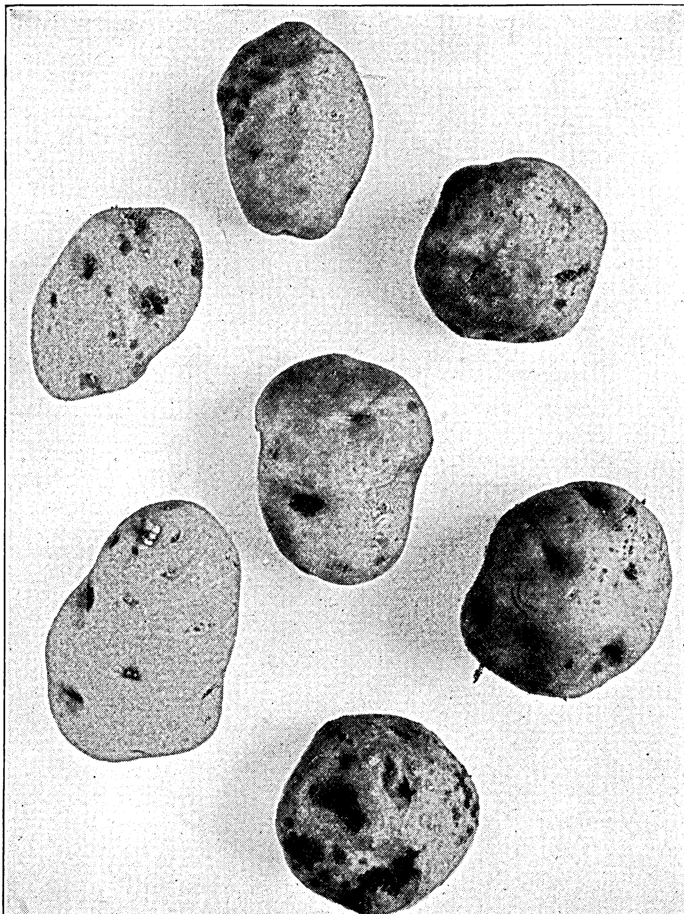

Plate 3. Early Ohio Seedling that Produces Smooth Tubers in the Same Plot

By selecting the smooth-tubered Early Ohio seedlings and again selecting the smooth-tubered seedlings in their inbred progeny, the undesirable character for second growths can be eliminated.