

GENETIC VARIATION AMONG HAPLOIDS OF THE COMMON POTATO

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INTRODUCTION

A considerable degree of genetic variability may be expected among haploids ($2n=24$) of the common potato, *Solanum tuberosum* L. ($2n=48$). This reasoning is based upon the knowledge that [1] commercial varieties of *S. tuberosum*, as well as breeding selections of this species, are highly heterozygous (9, 10, 11); [2] reduction in ploidy results in an increased potential for expression of variability; and [3] haploidy provides a rapid means of inbreeding (5).

Genetic variability found among the 28 'raw' or "primary" potato haploids previously reported (4, 6) plus one additional haploid of Katahdin will be described in this paper. Genetic variability of "secondary" haploids, $2n=24$ progeny resulting from inter-mating the "primary" haploids, will be reported at a subsequent date.

DESCRIPTION OF *Solanum tuberosum* HAPLOIDS

Twenty-two of the 29 haploid plants were derived, following interspecific matings, from the commercial variety Katahdin. Where possible, and unless otherwise indicated, comparisons made in this paper will either be between the haploids of Katahdin or between these 22 haploids and the parent Katahdin. The parentage of all haploids is listed in Table 1. Comparisons of vigor, plant size and tuber yield are based upon 1959 field trials at Sturgeon Bay, Wisconsin. Since the quantities of planting stock were very limited, no statistical treatment of these data has been attempted.

Plant Size and Vigor

The ranges of variability for plant vigor and size are striking (Fig. 1). A few plants, such as US-W5 and US-W8, are small and weak. The majority of the haploid selections have fair to good vigor and the mature plants are approximately $\frac{1}{2}$ to $\frac{2}{3}$ the size of the parent (Fig. 3). A few haploids, particularly US-W20 and US-W23, have very good vigor and equal or exceed the parent in size.

Leaves

The inter-haploid variability for leaf size and shape is considerable. Leaves of the haploids are, with two exceptions (US-W7 and US-W20), noticeably narrower and smaller than those of the parent Katahdin (Fig. 2). The leaves of the haploids are generally lighter green than those of the parent and in three instances, US-W5, US-W8 and US-W26, are somewhat chlorotic.

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TABLE 1.—*Ovule fertility of Solanum tuberosum haploids.*

Haploid	Parent	Haploid ♀ X <i>S. phureja</i> (P.I. 195198) ♂			
		Flowers pollinated	Fruit	Seeds	Seeds/Fruit
US-W1	Katahdin	7	4	826	208
US-W2	Minn. 44-2	15	8	21	3
US-W3	Minn. 15-2-10-1-2	45	38	2136	56
US-W4	Minn. 20-20-34	12	10	896	90
US-W5	Minn. 113-1	6	5	699	140
US-W6	Minn. 20-20-34	2	2	282	141
US-W7	Katahdin	23	16	745	47
US-W8	Katahdin	No flowers	..	..	..
US-W9	Katahdin	No flowers	..	..	..
US-W10	Katahdin	5	3	124	41
US-W11	Katahdin	9*	4	199	50
US-W12	Katahdin	8	6	260	43
US-W13	Katahdin	10	2	76	38
US-W14	Katahdin	19	9	493	55
US-W15	Katahdin	6	1	31	31
US-W16	Katahdin	No flowers	..	..	..
US-W17	Minn. 10-5-12	3*	2	10	5
US-W18	Katahdin	No flowers	..	..	..
US-W19 (lost)	ND 457-1	..	..	..	..
US-W20	Katahdin	7*	4	215	54
US-W21	Katahdin	10	3	102	34
US-W22	Katahdin	5	0	0	0
US-W23	Katahdin	2	2	217	109
US-W24	Katahdin	23	4	77	19
US-W25	Katahdin	10	6	253	59
US-W26	Katahdin	No flowers	..	..	..
US-W27	Katahdin	11	10	530	53
US-W28	Katahdin	18	1	36	36
US-W29	Katahdin	16	14	1737	124

*Flowers were pollinated with a different selection of *S. phureja*.

Flowers

All 6 of the haploids from the Minnesota breeding stocks and 17 of the 22 Katahdin haploids have flowered to date. Most of the haploids flower less and for a shorter period than Katahdin. Two haploids, however, US-W29 from Katahdin and US-W3 from Minn. 15-2-10-1-2, flower heavily for 3 weeks or more of the summer growing season. Under the short-day conditions of fall, winter and early spring, most of the haploids tuberize very rapidly and fail to flower. As in the parents, flowering may be induced in many selections during this period by lengthening the photoperiod with artificial light. Of the Katahdin haploids, 9 have white flowers and the remainder are pigmented ranging in color from light to dark pink.

Fertility

Twenty-two of the 23 haploids that have flowered have been used successfully as female parents (Fig. 5). Two haploids, US-W1 from Katahdin and US-W4 from Minn. 20-20-34, are functional as both male and female parents in inter-haploid matings as well as in matings with

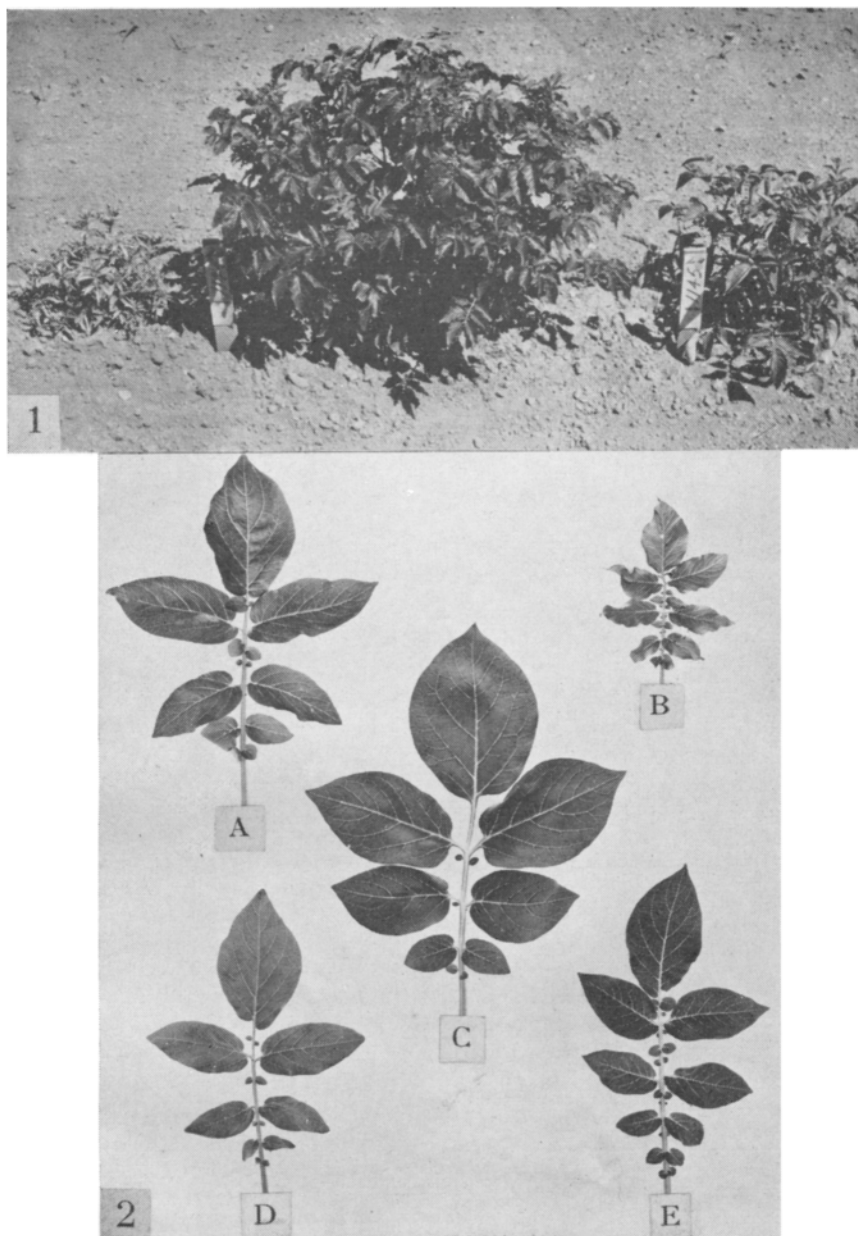


FIG. 1.—*S. tuberosum* haploids: Left to right—US-W5, US-W6 and US-W7.

FIG. 2.—Leaves from the variety Katahdin and from its haploid offspring:
A) US-W7; B) US-W13; C) Katahdin; D) US-W1; E) US-W9.

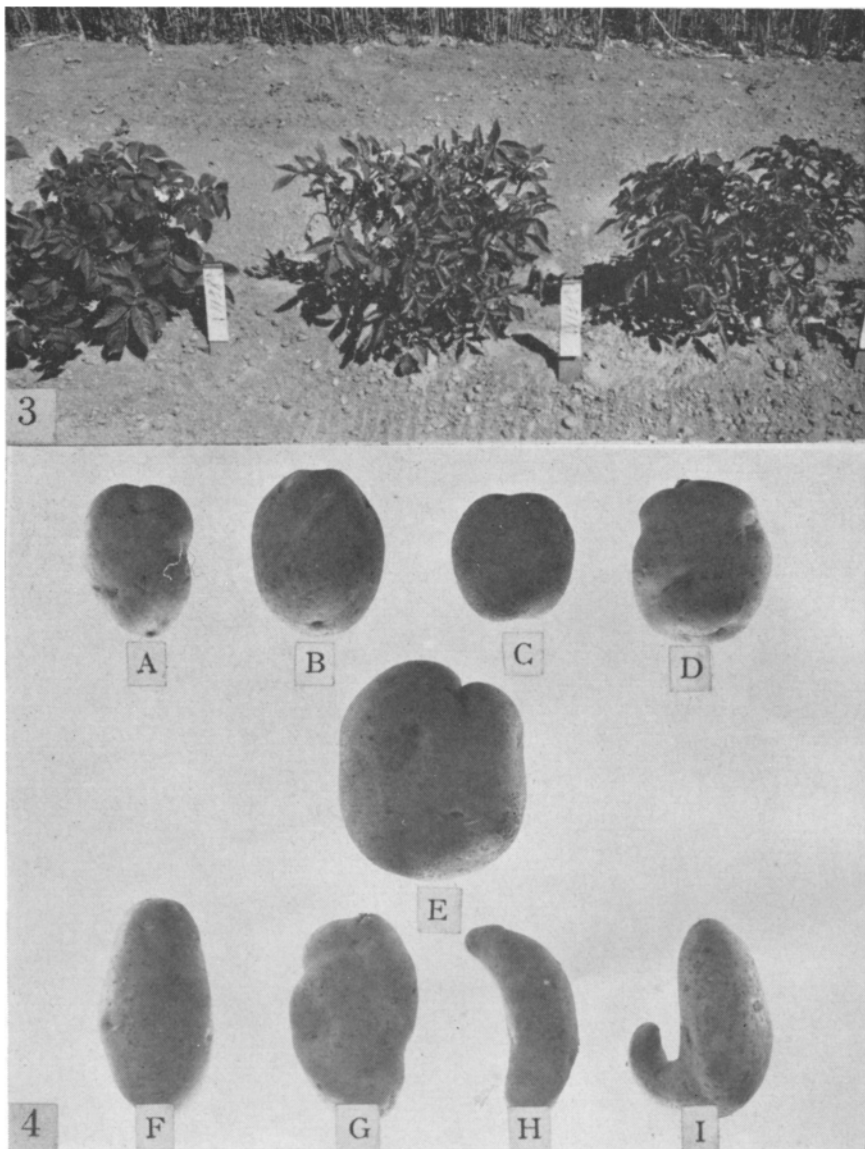


FIG. 3.—*S. tuberosum* and haploids: Left to right—variety Merrimack, US-W1 and US-W2.

FIG. 4.—Tubers from the variety Katahdin and from its haploid offspring:
A) US-W1; B) US-W12; C) US-W15; D) US-W23; E) Katahdin;
F) US-W22; G) US-W20; H) US-W24; I) US-W28.

certain haploids ($2n=24$) *Solanum* species. Pollen stainability of the haploids ranged from 0-20 per cent for the male-sterile individuals and from 60-80 per cent for the male-fertile individuals. The variation in pollen stainability among the haploids is illustrated in Figs. 6-9.

The criterion employed for judging the female fertility of the haploids is the production of viable seed following matings with the cultivated South American species *Solanum phureja* ($2n=24$). Data concerning the ovule fertility of the haploids are summarized in Table 1. Inter-haploid matings have not been used as a measure of fertility because [1] there is evidence of genetic incompatibility in some of the haploid-haploid matings and [2] as previously noted, most of the haploids which have flowered to date do not normally have sufficient stainable pollen for male fertility.

A study of meiosis and crossability in haploids US-W1 and US-W3 was previously reported (12).

Tubers

The inter-haploid variability for number, shape, size and yield of tubers is very marked. The range of shapes among the Katahdin haploids include round-oval (US-W12, US-W15, US-W23), long-rough (US-W20), long-smooth (US-W22), pear-shape (US-W1) and hook-neck squash (US-W24, US-W28). The shape of Katahdin is superior to that of the majority of its haploid offspring (Fig. 4). The number of tubers per hill ranged from 6 (US-W13, US-W18) to 33 (US-W23) with most haploids having 10-15. A light russetting of the tubers occurred on one haploid of Katahdin (US-W15).

Tuber size and yield of the haploids are usually considerably smaller than the parent. However, two haploids, US-W20 and US-W23, produced in 110 days individual hill yields of $3\frac{1}{4}$ -4 and $3\frac{1}{2}$ - $3\frac{3}{4}$ pounds, respectively, as compared with $4\frac{1}{2}$ -5 pounds of the parent Katahdin. In a later harvest (124-day growing season) the haploid US-W20 produced an individual hill yield of 7 pounds as compared with $5\frac{3}{4}$ pounds of the parent. One haploid from Katahdin, US-W29, had not set tubers at the time of harvest, but it does set tubers in the greenhouse under short-day conditions.

DISCUSSION

Changes in the ploidy of plants usually results in an increase or decrease in vigor and size. Induced tetraploids, for example, are generally larger in one or more plant parts than their diploid parents (2, 13, 14). Higher levels of ploidy, on the other hand, may result in loss of vigor and dwarfness. Johnstone (7) reported this in induced octaploids ($2n=96$) of common potato varieties ($2n=48$). The total yield of tubers, as well as the tuber size, of these octaploid potatoes was reduced.

Reductions in ploidy arising from reduced parthenogenesis also result in loss of vigor and size in the haploid offspring of most plant species (8). This is the case with all but one of the 22 haploid plants derived from the potato variety Katahdin. The one exception, US-W20, equalled the parent in vigor and exceeded it in tuber yield in a 124-day growing season.

The loss of vigor and size, which usually characterizes reduction in ploidy, is but a partial measure of the total genetic consequence of

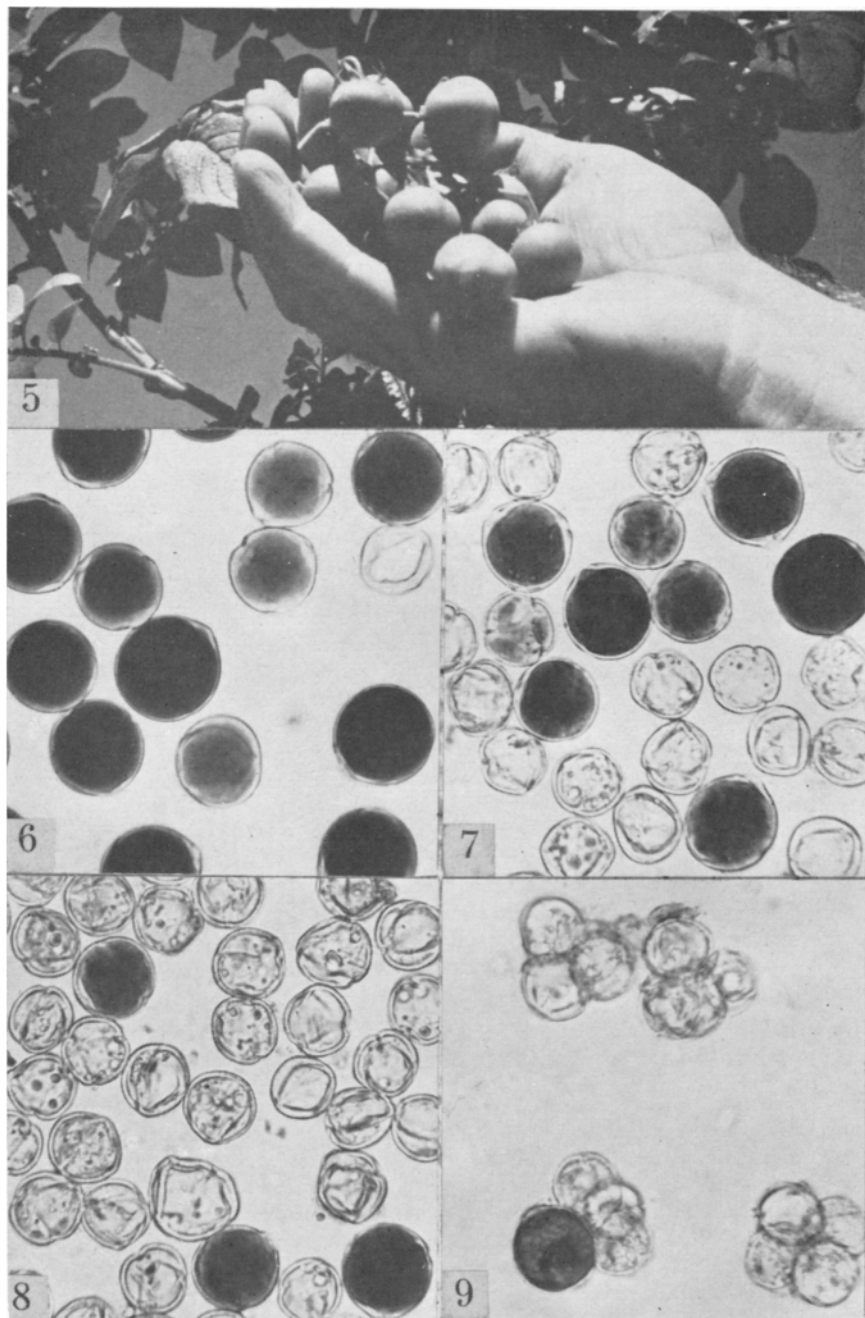


FIG. 5.—Fruits resulting from pollination of US-W29 flowers with pollen from *S. phureja*.
 FIG. 6-9.—Pollen of *S. tuberosum* haploids stained with aceto-carmin: 6) US-W1; 7) US-W29; 8) US-W14; 9) US-W20.

haploidy. Haploidy also allows for increased potential in the expression of genetic variability. The specific amount of variability expressed among the haploids derived from a particular parent is dependent upon the genetic nature, especially the heterozygosity and ploidy, of the parent. Obviously, much greater variability would be expected among the haploids from a heterozygous parent than from one which is relatively homozygous. The level of ploidy as well as the nature of the ploidy of a parent will also influence the variability expressed among its haploid offspring. A difference would be expected, for example, in the degree of variability among the haploids, *i.e.* monoploids, from a diploid parent and among the haploids, *i.e.* diploids, from its induced autotetraploid. This difference may be attributed in part to the differential in inbreeding due to haploidy. About seven generations of selfing a diploid are required to approximate the amount of inbreeding obtained through the extraction of haploids, *i.e.* monopolids, from such a diploid parent. Three generations of selfing an autotetraploid are required to approximate the degree of inbreeding obtained through the extraction of haploids, *i.e.* diploids, from such an autotetraploid parent. It should be further noted that each haploid derived from a diploid carries but one genome and consequently is completely homozygous. By contrast each haploid derived from an autotetraploid carries two genomes and as a result the occurrence of a completely homozygous haploid, *i.e.* diploid, considering the probable magnitude of heterozygosity in most autotetraploids, would be a very rare event. These latter relationships may be illustrated by considering the frequency of homozygous individuals expected among the haploids derived from a diploid of the genotype AaBb, in other words, the frequency of homozygous gametes expected from such a genotype, as compared with the expected frequency of homozygous haploids (calculated from the expected gametic frequency) from the induced autotetraploid, AAaaBBbb. The calculation of the gametic frequency of the autotetraploid assumes random chromosome segregation.

<i>Parental Genotype</i>	<i>Expected Gametic Frequency</i>			
Diploid—AaBb	1/4AB	:1/4Ab	:1/4aB	:1/4ab
Induced				
Autotetraploid—				
AAaaBBbb	1/36AABB	:1/36AAbb	:4/36AABb	:4/36AaBB
	:16/36AaBb	:4/36Aabb	:4/36aaBB	:1/36aaBB
		:1/36aabb		

From a comparison of these gametic frequencies it may be seen that in the diploid parent with the genotype AaBb four classes of haploids each with the same expected frequency and each completely homozygous will occur. In the case of the autotetraploid parent nine classes of haploids will occur, only four of which are completely homozygous. The expected frequency of these four homozygous classes combined is only 1/9 ($1/36AABB + 1/36AAbb + 1/36aaBB + 1/36aabb$).

The genetic nature of *S. tuberosum* must be borne in mind in considering the effects of haploidy in the potato. First, this species is considered an autotetraploid by most investigators (1, 3, 9, 11). Second,

most selections of the common potato, especially the commercial varieties, are highly heterozygous (10, 11). Hence considerable variability would be expected among the haploid offspring of potato due to the close inbreeding of a highly heterozygous parent. This expectation has been realized in the variability expressed among the 22 "raw" haploids of the variety Katahdin.

It should be re-emphasized, however, that due to autotetraploidy only a portion of the inherent variability of the potato will be expressed in populations of its "raw" haploid offspring. This aspect will be dealt with in greater detail in a subsequent paper, however, one simple example will be drawn to illustrate this point.

Make the following assumptions: [1] the autotetraploid parent carries genes in the triplex condition (AAAa), [2] dominance is complete at both the diploid and the tetraploid level, [3] the inheritance pattern of the gene in question is conditioned by random chromosome segregation; then the "raw" haploids extracted from such triplex genotypes will be of two genotypes, AA and Aa. Hence, the genetic variability due to the action of the recessive gene "a" would not be expressed among the "raw" haploids. Such variability would be expressed, however, among selfed and sib-mated populations of the "raw" haploids or among monoploids from such "raw" haploids.

SUMMARY

1. Genetic variability among 29 haploids ($2n=24$) of the common potato ($2n=48$) is described.

2. Plant parts of the haploids are reduced in size, with few exceptions, as compared with those of the parent.

3. The tuber yields of the haploid plants are in general, considerably less than those of their parents. One notable exception, however, is the haploid US-W20, which in an initial limited trial outyielded its parent Katahdin in a 124-day growing season.

4. Twenty-two of the 23 haploids that flowered are functional as female parents. Two haploids, US-W1 from Katahdin and US-W4 from Minn. 20-20-34, are functional both as male and female parents in inter-haploid matings as well as in matings with *Solanum phureja* ($2n=24$).

5. Certain genetic consequences of haploidy are discussed.

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