Cytological studies on potatoes with some remarks on genetical experiments. Part II.

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Genetical experiments

1. Frost resistance and maturity

For the purpose of securing the above physiological character, *Solanum demissum* L. and *S. tuberosum* L. were used. As already reported, *S. demissum* has 72 diploid chromosomes with normal meiotic division, and *S. tuberosum* is usual tetraploid form having 48 diploid chromosomes. The parents differed from each other in many characters (Table 14).

Table 14. A comparison of morphological characters in *S. demissum* L. and *S. tuberosum* L.

Character	<i>S. demissum</i>	<i>S. tuberosum</i>
Cotyledon width	narrow	wide
Cotyledon length	long	short
Terminal leaflet width	narrow	wide
Mature leaf area	small	large
Mature stem height	short	long
Internode length	short	long
Mature stem diameter	small	large
Mature stem habit	prostrate	erect
Stolon length	long	short
Tuber size	small	large

Plants of *S. tuberosum* matured in late August, while all plants of *S. demissum* were still green during October. *S. demissum* was not injured by the first frost or snow of the year in early November which killed *S. tuberosum*.

In 1946, crosses between *S. demissum* and *S. tuberosum* were carried out. 51 plants making up the F₁ family were started in the green-house in the early spring of 1947 and grown there for 3 months before being moved to the field. They were alike in general appearance and were intermediate in external characters as contrasted with their parents, though within their progenies a certain range of variation exists. Hybrid vigor was especially noticeable. In 1948 and 1949, 1150 F₂ plants were grown from seeds of F₁ plants (A-10, 11, 12, 20, 21 and 22). Out of 1150 plants, 654 were used for the experiment of frost resistance and the remaining 496 were used for maturity. These plants were similar to each other and resemble *S. tuberosum* in

general appearance. Several morphological and physiological characters were measured. The physiological results were given in table 15 and table 16.

Table 15. Segregation for frost resistance in F_2 .

Family No.	No. of plant used	Degree of injury*			
		None	Medium	Severe	Dead
A 10-1	44	10	21	13	
-2	54	14	28	12	
-3	40	10	19	11	
-4	50	11	26	13	
A 11-1	52	14	26	12	
-2	37	8	20	9	
-4	41	9	21	11	
-5	51	13	24	14	
A 12-1	60	15	29	16	
-2	37	8	20	9	
-3	55	14	29	12	
-4	50	11	26	13	
-5	45	10	24	11	
-6	38	8	19	11	
Total	654	155	332	167	
Observed ratio		0.948	2.031	1.021	
Expected ratio		1	2	1	
Deviation		0.052	0.031	0.021	

*Frost injury was recorded on October 30 and on November 5.

Table 16. Segregation for maturity in F_2 .

Family No.	No. of plant used	Degree of maturity*		
		Mature	Medium	Unmature
A 20-1	40	11	19	10
-2	37	10	19	8
-3	29	7	15	7
-4	28	8	13	7
-5	41	9	21	11
A 21-1	35	9	18	8
-2	31	8	15	8
-4	36	7	20	9
-5	28	8	14	6
A 22-1	41	11	21	9
-2	35	9	18	8
-3	42	14	20	8
-4	34	10	17	7
-5	39	12	19	8
Total	496	133	249	114
Observed ratio		1.073	2.008	0.919
Expected ratio		1	2	1
Deviation		0.073	0.008	0.081

* Maturity was recorded on September 1 and 15.

Frost injury was recorded on October 30 at Kuchyan and on November 5 at Sapporo. At this season *S. demissum* showed no injury from the light frost, while all plants of *S. tuberosum* were killed. On the other hand, F_2 plants showed a complete range from no injury to lethal as shown in table 15. Maturity records were taken on September 1 at Sapporo and on September 15 at Kuchyan. At this time *S. demissum* was still green, while all plants of diploid, triploid and tetraploid *S. tuberosum* were already mature, and F_2 plants showed a complete range from mature to green as given in table 16.

Though the exact discrimination may be difficult, it can be seen from the above data that the frost resistance and maturity in potato exhibit an incomplete monogenic difference, giving in F_2 an approximate ratio of 1 : 2 : 1.

2. Fresh and tuber color

Materials used for this experiment were as follows :

Diploid *S. tuberosum*. Fresh color is yellow.

Tetraploid *S. tuberosum*. Fresh color is white.

These 2 varieties were used for fresh color inheritance.

Tetraploid *S. tuberosum*. Tuber color is red.

Tetraploid *S. tuberosum*. Tuber color is yellowish white.

These 2 varieties were used for tuber color inheritance.

In order to ascertain the color inheritance of fresh and tuber, several crosses were made. The F_1 plants had fresh like the yellow type and in F_2 there was segregation into yellow and white in a ratio of 3 : 1. Results are summarized in table 17.

Table 17. Segregation for fresh color in F_2 .

Family No.	No. of plants used	White	Yellow
B 10-1	30	8	22
-2	40	11	29
-3	34	8	26
-4	51	13	38
-5	42	11	31
B 11-1	36	8	28
-2	44	12	32
-3	57	15	42
-5	43	11	32
B 12-1	31	8	23
-2	29	7	22
-3	45	13	32
-4	53	14	39
-5	35	10	25
Total	570	149	421
Observed ratio		0.046	2.954
Expected ratio		1	3
Deviation		0.046	0.046

As will be seen in table 17, it seems likely that yellow is a monogenic dominant over white.

The crosses in tuber color experiments, red $\times$ white, gave purple in F_1 and a ratio of 9 purple : 3 red : 4 white in F_2 . A summary of the results is given in table 18.

Table 18. Segregation for tuber color in F_2 .

Family No.	No. of plants used	Purple	Red	White
B 20-1	35	19	7	9
-2	40	24	7	9
-3	28	16	4	8
-4	34	20	6	8
-5	45	26	9	10
B 21-1	37	20	8	9
-2	50	26	10	14
-3	46	25	9	12
B 22-1	42	23	8	11
-2	47	23	9	15
-3	29	17	5	7
-4	37	19	7	11
B 23-1	49	25	8	16
-3	38	24	6	8
-4	27	15	5	7
-5	34	22	6	6
-6	37	20	8	9
Total	655	364	122	169
Observed ratio		8.892	2.980	4.128
Expected ratio		9	3	4
Deviation		0.108	0.020	0.128

This result may be explained on a digenic basis. The genic scheme was represented as :

AB	Purple	9
Ab	Red	3
aB	White	4
ab		

A is a gene originating color, its absence resulting in white flowers. B is a gene causing, together with A , uniform distribution of color on the under surface, its absence causing distribution of color on the upper surface.

3. Pollen sterility

As already described, the author discovered 1 apparently healthy but perfect male sterile potato. This plant readily functioned as female parent and no difficulty was found in obtaining fruit and seeds when pollen of normal fruitful plants was applied. On the other hand, the mature pollen produced by this plant is nearly normal in amount, but its development is arrested.

In 1946, a cross was made between male sterile and a different unrelated male fertile parent. The cross yielded many seeds, which germinated rather well, but some seedlings died before being moved to the field. All F_1 plants were self-fruitful, and all those tested had normal pollen and F_2 plants gave a segregation of a 3 : 1 ratio as given in table 19. Male sterility was completely recessive. But the results obtained from the other cross experiment suggested that male sterility was not a simple recessive. The ratio for male fertile and male sterile among the F_2 progenies of male steriles $\times$ unrelated male fertile potatoes grown in 1947 and 1948 is shown in table 20. All closely approach the digenic ratio, 15 : 1. These results, therefore, indicate that male sterility probably depends on 2 recessive genes. Adopting the symbols used in maize, the genes are termed ms_1 and ms_2 . Male-sterile plants are homozygous for both these recessive genes, and male-fertile plants contain either one or both of the dominant alleles MS_1 and MS_2 .

Table 19. Segregation for male-sterile in F_2 (1946).

Family No.	No. of plants used	Male-fertile	Male-sterile
C 10-1	36	28	8
-2	42	32	10
-3	39	29	10
-4	41	30	11
-5	29	22	7
-6	28	21	7
-7	39	31	8
-8	47	36	11
Total	301	229	72
Observed ratio		3.043	0.957
Expected ratio		3	1
Deviation		0.043	0.043

Table 20. Segregation for male-sterile in F_2 (1947-1948).

Family No.	No. of plants used	Male-fertile	Male-sterile
C 20-1	29	27	2
-2	40	37	3
-3	39	37	2
-4	37	35	2
-5	46	43	3
C 21-1	30	28	2
-2	49	45	4
-4	35	33	2
-5	51	47	4
-6	33	31	2
C 22-1	27	25	2
-2	46	43	3
-3	38	35	3
-4	35	33	2
-5	43	39	4
Total	578	538	40
Observed ratio		14.893	1.107
Expected ratio		15	1
Deviation		0.107	0.107

As will be seen in table 19 and 20, the male fertile plant used in the former experiment suggests that it is heterozygous for at least one of the male-sterility genes. And it is suggested that some of the unfruitful potato plants are male fertile segregates from the selfing of fruitful and apparently normal heterozygous plants.

Discussion

As will be clear from the table 1, potato consists of a polyploid series with 12, 18, 24, 30 and 36 as their haploid chromosome number. As is known, all wild species and cultivated varieties in potato are multiples of 12 haploid chromosomes and many workers concluded that 12 is the basic number in potato. From the present study, however, the question has therefore been raised as to the basic chromosome number. As mentioned already, the secondary association in diploid, triploid and tetraploid potatoes was observed commonly. In diploid form, there is almost exclusively association in groups of 2 bivalents, in addition to single bivalents. In the triploid, there is a definite new class of association, groups of 3 bivalents, and in tetraploid, groups of 2, 3 and 4 bivalents are frequent. In tetraploid *Solanum tuberosum*, Meurman and Rancken (1932) and Propach (1937) also mention the occurrence of secondary association. Müntzing's results (1933), however, are parallel with those observed by the present author. He has definitely shown that secondary association is not only of tetraploid and triploid varieties, but also of diploid *S. tuberosum*. But Meurman and Rancken do not believe that secondary association takes place in diploid *Solanum* and refer to the drawings of Jørgensen (1928), Vilmorin and Simonet (1917). In addition to Müntzing and the present author's observations, however, the author refers to Rybin (1930) and some others' papers. Their drawing and microphotograph of chromosomes in PMCs from diploid forms show clearly the secondary association just as in diploid forms observed by the author. Here the secondary association is the definite phenomenon in potato. The maximum association hitherto found by Müntzing, 5 groups of 2 bivalents was only observed once. In the present study, 6 groups of 2 bivalents was newly demonstrated here by the author. And in addition to this phenomenon of secondary association, groups consisting of 6 bivalent or univalent chromosomes were also first demonstrated in the meiotic division of hybrids from *Solanum demissum* ($2n=72$) $\times$ *S. tuberosum* ($2n=48$). The possible occurrence of these sorts of association suggests that 6 rather than 12 may be the primary basic number in potato and that 12 is secondary origin.

The polyploids are usually divided according to their ancestors into 2 classes: autopolyploids and allopolyploids. And it can be said that both phenomena, autopolyploidy as well as allopolyploidy, have played a very prominent rôle in evolution in potato. In many cases, it is difficult to determine to which class of polyploids the different species of potato dealt with in this paper are to be referred. However, the observations of secondary association and no multivalent formation presented in this paper, give a evidence for this problem. According to Lawrence (1931), the secondary association is especially characteristic of allopolyploids, true multivalent

formation of autopolyploids. From these reasons, potato, especially diploid form and most of tetraploid forms may be allopolyploids derived from 2 or 4 original basic species having 6 as the basic chromosome number belonging to 2 or 4 different ancestral genomes. And the author is at variance with the opinion of Fukuda (1927) who considers the cultivated *S. tuberosum* to have arisen from only one species. The opinion of the hybrid origin of polyploid cultivated potatoes is strengthened by the existence of a group of closely related polyploid wild forms. The chromosome configuration in *Solanum maglia* and *S. commersonii* being wild triploid species, seems to indicate that these plants are of natural hybrids from the interspecific cross, tetraploid form $\times$ diploid. And they are almost similar with the meiotic behavior of the artificially produced triploid hybrid, *S. acaule* ($2n=48$) $\times$ *S. caldasii* ($2n=24$).

A survey of cytological literature on potato shows that it is unusual to find species, especially *S. tuberosum*, represented by diploid, triploid and tetraploid form. Cultivated *S. tuberosum* have mostly 24 as their haploid chromosome number. All 40 varieties except 1 diploid and 1 triploid investigated in the present study, have also 24 haploid chromosomes, and Fukuda (1927), Longley and Clark (1930) and Rybin (1929, 1930) gained the similar results. But a few varieties having lower chromosome number, $n=18$ and 12 were reported by Rybin (1930), Müntzing (1933) and the present author. And Rybin found among the local cultivated potato varieties of Central America and South America forms with 12, 18 and 24 haploid chromosomes. Müntzing states that diploid and triploid representatives of *S. tuberosum* have a limited distribution area in Peru and Bolivia.

The irregular meiotic divisions in tetraploid potatoes having $n=24$ chromosomes, especially cultivated *S. tuberosum*, were commonly observed in the present study. This phenomenon varies from regular in a few to extremely irregular in many varieties and on the basis of variation in chromosome behavior, the tetraploid varieties were separated into the following 5 groups: (1) Varieties in which meiosis is rather regular and both the 1st and 2nd divisions are completed. (2) Varieties in which there are frequently some univalent chromosomes among the bivalents, but in which both the 1st and 2nd division usually occur. (3) Varieties in which there are frequently some univalents, with an occasional cell showing no pairing and in which there are some cells that go through one division only. (4) Varieties in which PMCs rarely go beyond one division and a number of the cells show no pairing of chromosomes. (5) Varieties in which a large percentage of the cells show the somatic chromosome number and in which true meiosis is frequently absent. And the nucleus degenerates in the prophase or metaphase and the cell divides in an amitotic manner. The similar results were also described by Fukuda (1927), Longley and Clark (1930) and others. These striking differences of normality in one species may be considered to be due to the following reasons: the cultivated potato, especially *S. tuberosum* includes many varieties and new varieties are being produced constantly. The older varieties run out in the course of time are supplanted by new ones. The running out is largely due to the fact that growers, as a rule, do not practise seed-selection. The new varieties are ordinarily

produced either from hybridized seeds or from bud-sports, but most of them are due to breeding. And the present study suggests that the cultivated varieties have a mixed ancestry and that the ancestors are to be found not in a single wild species but in two or more. If these hybrids were to propagate asexually, polyploid forms showing various grades of irregularity would be established. In potatoes, however, the asexual reproduction is a common, so that many cultivated forms of *S. tuberosum* which vary from regular to extremely irregular may be preserved to this day.

2 wild forms, *S. maglia* and *S. commersonii* and 1 cultivated variety, *S. tuberosum* were found to be triploid. But their chromosome configurations in PMCs were quite different. In the former, no multivalents were formed, and all chromosomes as bivalents showed 7 types of chromosome configuration. Longley and Clark (1930) also reported the same result on meiosis in wild triploid forms. The chromosome configuration seems to indicate that the wild triploids are allotriploid derived from the interspecific cross, tetraploid form $\times$ diploid and they are almost similar with the meiotic behavior of the triploid hybrids which are artificially produced by the author. In the latter, trivalents were often observed and their frequency was rather high. The same observation on triploid *S. tuberosum* was made by Müntzing (1933). In triploid tomato ($2n=36$), Jørgensen (1928) reported that 12 trivalents are present at diakinesis and are rare at metaphase, and that sometimes only 2 or 3 are formed. In triploid *Datura* ($2n=36$), Belling and Blakeslee (1922) found that triploid formation is completed and in triploid *Primula* having the same 36 chromosomes, varies from 7 to 12 (Dark, 1931). As is now well-known, the relative frequency of trivalents, bivalents and univalents is dependent on the frequency and nature of chiasmata. Plants in which the chiasma are frequent and interstitial will show more trivalents than plants with a low number of terminal chiasmata, and within the same chromosome complement, the small chromosomes will show a lower frequency of trivalents than the longer chromosomes. In potato, the number of chiasmata is very low and only terminal chiasmata were observed. At 1st metaphase, trivalents are united by 1 terminal chiasma and trivalents are, as a rule, either of the triple chain type or Y type with a triple terminal chiasma. In tetraploid *S. tuberosum*, Meurman and Rancken (1932) have observed tetravalents and multivalents of more than four chromosomes and they state that its chiasmata are also terminal. To explain this phenomenon, Müntzing (1933) states that segmental interchange has occurred in the ancestry of the forms examined by them. In triploid *S. tuberosum*, the fact that in spite of the low frequency of terminal chiasmata, the formation of trivalents is rather high, strongly indicates that their 3 genomes must be similar and this variety may be an autotriploid. In the 1st anaphase, lagging chromosomes were often observed and most of them split at the equator after the bivalents had passed to the pole. The 2nd division is usually clean. In triploid tomato, on the other hand, Lesley (1926) states that the 1st division is usually clean and lagging chromosomes are rare. In the 2nd division more laggards were observed.

Before the secondary association in potato was first demonstrated by Müntzing (1933), no positive proof of it was recorded in the literature and especially in diploid form,

some worker denied the secondary association. It may be quite conceivable that the reproduced drawings do not reveal any secondary association because, as Lawrence (1931 a) points out, "the cytologists always choose the best plate to draw, i.e. the plate which shows the most even distribution of chromosomes in polar view". Since the theory of secondary association was first demonstrated by Darlington (1928), this theory has been subjected to a great deal of criticism. The critics, particularly Nebel (1931, 1933) and Sax (1931), explain the phenomenon essentially as fixation artefacts and usually call it "clumping". But there is in reality no definite foundation to deny it and recently the existence of secondary association in meiotic chromosome has been generally elucidated by many workers. It has been definitely accepted that the secondary association of meiotic chromosomes manifests the chromosome homology in hybrids which are secondary balanced polyploids derived from ancestral forms. The present investigation has definitely shown that secondary association in potato is characteristic, not only of tetraploid and triploid forms, but also of diploid. Müntzing (1933), from his observation, also pointed out that the secondary association takes place in diploid, triploid and tetraploid *S. tuberosum* commonly, and in addition to this observation, he refers to the drawings of Longley and Clark (1930) and Rybin (1930.). The types and frequencies of secondary association tested by Müntzing are generally parallel with the present result, but the maximum association in diploid form differs from the author's result. The maximum association observed by him is 5 groups of 2 bivalents and 2 single bivalents. But nevertheless in the author's case, 6 groups of 2 bivalents and no single bivalents were maximum associated type. From this evidence, it is more probable that 6 is the primary basic number in potato and 12 is the secondary origin. Then, the genom formulae of diploid set may be written AAAIAI.

Hitherto no aneuploid potato has been found so far as the author is aware. In the present study, 23 aneuploid potatoes were newly demonstrated here. 3 of them were found in natural condition and the others were artificially induced by the hybridization and low temperature treatment. It is noteworthy that aneuploidy is also present in potato. In Cyperaceae, Heilborn (1924, 1932) and Håkansson (1929) offered the following 3 facts as a probable explanation of aneuploidy: (1) transverse division of single chromosome, (2) duplication of entire chromosomes, (3) hybridization. The present aneuploids found in natural condition, show the irregular meiotic division and the chromosome behavior of these aneuploids is very similar to that described for cultivated varieties. From these points of view, most probably these aneuploids would have been of hybrids derived from crosses, union of aneuploid gametes such as $n+1$, $n-1$ and etc. The new varieties in potato are ordinarily produced either from hybridized seeds or from buds-sports. They are being produced constantly and are permanently preserved by the vegetative propagation. Therefore, by the detailed investigation, it may be expected that the aneuploid potato is found more often than considered until now. There is no doubt that the evolution and formation of species is chiefly dependent upon qualitative alterations of chromosomes. And it can be said

to be definitely proved that both phenomena, aneuploidy as well as polyploidy, have played a very prominent rôle in evolution. Therefore, it is worthy of notice, from these points of view, that aneuploids found in potato have a prominent rôle of potato evolution or not. In 16 aneuploids induced by hybridization, however, there was no apparent relationship between chromosome number and tuber formation or seed production. But the relationship between the evolution and aneuploidy in potato must be reserved till further studies will be done.

Previously many investigators showed the effect of environmental factors such as high or low temperature change, X-ray, ultraviolet ray, centrifuging, aging seeds and etc. to nuclear and cell division. In the present study, the effect of low temperature has been examined in meiotic cells of diploid *S. tuberosum* with 12 pairs of normal chromosomes. And many irregularities such as chromatid fragmentation, fused chromatids, asynapsis and unbalance of nuclear and cell division, were detected. The effect of temperature on cell division has long been known, and the work has been done by many investigators: Belling (1925), Sakamura and Stow (1926), Michaelis (1926), Stow (1927), Shimotomai (1927), Takagi (1928), Koshochow (1928), Katayama (1929), Heilborn (1930), Randolph (1932), Hashimoto (1933), Peto (1935), Matsuda (1928, 1936), Müntzing (1936), Kironossowa (1936), Nakamura (1936), Dorsey (1936), Sax (1936, 1937), Shigenaga (1939), Swanson (1940), Darlington and La Cour (1940), Kawamura (1941), Griffiths (1941), Geitler (1941), Makino (1942), Kojima (1943), Haga (1943) and Okuno (1944). And these works were reviewed by the present author (1949). Chromosome aberrations, especially structural changes such as fragmentation, fusion, translocation and deficiency of chromosomes may be also induced by low temperature treatment as well as by high temperature, X-ray and aging of seeds. Peto (1935) found numerous fusions and some fragments in chromosomes of root-tips in *Hordeum* which had been subjected to heat. Kironossowa (1936) has reported that translocations are induced by subjecting seeds to a high temperature of 45° C. In *Aloe*, Camara (1935) found chromosome fragmentation, fusion and also inversion. Nawaschin and Gerassimowa (1936) suggested that these chromosome fragment, translocation and other abnormalities appear much like those induced by aging of seeds and X-ray. The present experiments on potato showed that the low temperature also induces various structural changes in chromosomes and asynapsis or suppression of chromosome segregation at meiosis which are often induced by high temperature, X-ray and etc. As these results, diploid or tetraploid pollen grains are often observed. Several authors have already demonstrated such an acceleration of chromosome behavior in meiosis through the effect of high or low temperature treatment, namely, Sakamura and Stow (1927) in *Gagea*, Stow (1927) in potato, De Mol (1923, 1928) in *Tulipa*, Takagi (1928) in *Lychnis*, Koshochow (1928) in *Zea* and *Cucumis*, Heilborn (1930) in *Malus*, Bleier (1930) in *Triticum*, Matsuura (1935) in *Oryza*, Matsuda (1928, 1936) in *Petunia*, Sax (1936) in *Rhoeo*, Dorsey (1936) in *Triticum* and *Secale*, Müntzing (1936) in *Hordeum*, De Mol (1936) in *Hyacinthus* and Matsuura (1937) in *Trillium*. And the effect of low temperature in producing polyploid gametes was first demon-

strated by Belling (1925). He found that low temperature would induce giant pollen grains in *Uvularia*, *Stizolobium* and *Datura*. The same results were also observed by the following authors: Michaelis (1926) in *Epilobium*, Shimotomai (1927) in *Liriope*, Straub (1936) in *Rhoeo*, Akemine (1937) in *Rhoeo* and Okuno (1946) in *Brassica* and *Begonia*. Nakamura (1935) found that the abnormal air temperature is occasionally sufficient to induce chromosome doubling. Cell division without nuclear division or nuclear division without cell division was also observed in the present experiments. Such abnormalities may be induced artificially by many agents, including hypertonic and hypotonic solutions, lack of oxygen, temperature changes. Cowdry (1924) suggested, these agents may cause a change in the physiological condition of the cytoplasm, namely cytoplasmic viscosity.

The sterility in potato was reported by some workers and the explanation for its causes has to some extent been also offered. East (1908), Dorsey and Breeze (1910) found that there is a great variation in the amount of viable pollen produced by different varieties and that in many of them there is a large percentage of defective pollen and they concluded that the sterility of potato is mostly due to the abortion of pollen grains. Knight (1910) suggested that the sterility is purely physiological, and that if the energies of the plant are artificially turned away from tuber formation, the formation of the sexual organs and of the gametes will be immediately favorably influenced and become perfect. But East denies this hypothesis, and he is of opinion that sterility in potato may be due to the condition in mutations or of the hybrids. Wittmack (1908) pointed out that the sterility is due to the unfavorable climate, and partial nutrition. The sterility in potato, however, has been elucidated by Fukuda (1927). He suggested that the sterility in potato may be determined by the following factors: (1) total energy of the plants, (2) vegetative energy, (3) generative energy, (4) influence of environmental condition and (5) the different degree of fertility or sterility are caused by the various combinations of these factors enumerated above. Sakamura and Stow (1927) and Stow (1927) suggested that high temperature affects the cultivated plant so strongly as to produce sterile pollen-grains. Young (1923) reported that the disintegration of nearly mature pollen-grains depends on the result of hereditary pollen sterility, and that unfavorable conditions induce its degenerative changes to take place at the earlier stages of development, accompanying the shedding of flower buds. Krantz, Becker and Fineman (1934) have also studied on the heritability of pollen sterility and they concluded that the inheritance of pollen sterility may be explained by assuming the presence of a tetrasomic gene which, when present in the pollen in the homozygous condition, is lethal and in the heterozygous condition partially lethal. As already mentioned above, the cultivated potato varieties show generally abnormal meiosis and as the result of this, various abortive gametes are induced. For this reason, it has often been thought that this irregularity is the direct cause for the potato sterility. It is not, however, the direct cause to explain the potato sterility, although it may be somewhat the response for the sterility. It should be remembered that pollen abortion is one

of factors responsible for fruiting in the cultivated common potatoes. The present results show that the fructification in potato does not depend upon the meiotic irregularity and it may be rather due to the environmental conditions, especially air temperature and the physiological nature of plant itself. The data presented in table 12 and 13 show that the fructification does not take place at the higher temperature than about 20°C which is an average temperature in day. The unfruitfulness may be due to the physiological unbalance, especially the ceasing of pollen tube growth on pistil. The degeneration involving both the anther and ovule induced by unfavorable climatic conditions was also demonstrated by the present study. Such degenerative change in ovule and anther may be mainly due to the shedding of flowers. And a male sterile potato was first demonstrated by the author. From the genetical experiment, it was found that male sterility is completely recessive and depends on 2 recessive genes. As above mentioned, some of other factors that influence fruitfulness in cultivated varieties are restricted habit of bloom, rudimentary to weak inflorescence, ready abscission of flowers, poorly developed stamens and the degeneration of many fertile ovules, and some of these appear to be due to the physiological unbalance induced by unfavorable climatic or environmental conditions and some one due to genes. Their presence lends support to the view that selection for high yield has favored the retention of genes adversely influencing sexual reproduction. On the other hand, continued sexual reproduction tends to eliminate these genes and selection is required to retain them.

Experiments on the inheritance of various characters in potato have been made by many investigators. However, only few genetical experiments on physiological characters have been done. Krantz (1922) made a cross between 2 late maturing potato varieties. In F_2 progenies, he observed the wide variation, segregates differing by more than 60 days in time of maturity. These results suggest that multiple genes are responsible for the maturing. Müller (1928) and Krantz and Hutchins (1929) have also obtained the same results. But as far as the present experiments are concerned, it can be seen that the frost resistance and maturing in potato exhibit an incomplete monogenic difference, giving in F_2 an approximate ratio of 1:2:1. Observations on the inheritance of tuber and flesh color have been made by several workers (Salaman 1910, 1911, East 1910, Fruwirth 1912, Wilson 1916, Asseyeva 1927, Köhler 1927). Most extensive works have been made by Sirks (1929). He assumed that there are 3 genes for skin and eye color, 2 of which, R and S are gene causing, together with both, the production of anthocyan in eyes and for skin color a third gene D is required in addition. And for purple color of skin and eye, he assumed a fourth gene P . The genic scheme was represented as follows:

	Skins	Eyes
$DP(R)S$	purple	purple
$DpRS$	red	red
$dP(R)S$	white	purple

<i>dpRS</i>	white	red
Others	white	white

On the fresh color, Fruwirth (1912) and Salaman (1910, 1911) found yellow dominant over white. On the other hand, Heribert-Nilsson (1913) showed that white is not always recessive. Krantz (1922), from a selfing of the purple fresh variety, obtained the following segregation: purple, medium purple and white in a 1:2:1 ratio indicating a monogenic difference between purple and white. Müller (1923), however, found a colored fresh variety which gave colored and white in a ratio of 9:7 by its selfing. When he made cross between this variety and a pure-breeding white variety, it gave in F_1 white-freshed progenies only. From this result, he assumed 3 genes: 2 genes, *C* and *I* are genes causing the formation of anthocyan in the fresh color and *Z* inhibits it. In the present experiment, however, it seems likely that yellow of the fresh is a monogenic dominant over white, and the inheritance of tuber color, red $\times$ white, may be explained on a digenic basis. As above stated, with respect to the skin and fresh color, different workers gained some different results. This cause may be depended on the difference of materials used. Potatoes, especially cultivated varieties are mostly hybrids which may be induced by crosses of 2 or more than 3 original basic species. This evidence has been cytologically elucidated by some workers and the present author.

In potato, very little is known of the inheritance in pollen sterility. Salaman (1910, 1912) and Heribert-Nilsson (1913) published papers on this subject. They believed that sterility is a monogenic dominant of fertility. Later evidence, however, indicated a more complex manner of inheritance (Salaman and Lesley, 1922). Krantz, Becker and Fineman (1939) made also some experiments on the inheritance of pollen sterility in cultivated potato (*S. tuberosum*). They assumed the presence of a tetrasomic gene which, when present in the pollen in the homozygous condition, is lethal and in the heterozygous condition partially lethal. In 1946, the author found a male sterile potato. This potato was crossed with 3 different unrelated male fertile parents. All F_1 progenies were selffruitful. Male sterility was completely recessive. In F_2 progenies of this experiments, 2 different segregations were obtained. One of them is distinctly near 3:1 (observed ratio 229:72) and the other 15:1 (observed ratio 538:40). These results, therefore, indicate that male sterility probably depends on 2 recessive genes. These genes were designated as *ms₁* and *ms₂*. This male sterile plant is homozygous for both these recessive genes, and male-fertile plants contain either one or both of the dominant alleles *MS₁* and *MS₂*.

Summary

In the present study, 14 wild species and 36 cultivated varieties and species were dealt with cytologically. They were found to constitute a distinct polyploid series, $2x-3x-4x-5x-6x$. Their polyploid relations are given in table 1.

Meiotic division in wild species takes place in the regular fashion in general, with 2

exceptions of triploid forms, *Solanum maglia* and *S. commersonii*, which have been considered as natural hybrids derived from a tetraploid form $\times$ diploid form. Pentaploid wild form, *S. demissum* forma *atrocyaneum*, also has meiotic irregularities, suggesting that it is a hybrid origin.

The meiotic behavior of 35 cultivated varieties (*S. tuberosum*) varies from regular in a few to extremely irregular. On the basis of variation in chromosome behavior, 35 varieties have been separated into 5 groups.

The secondary association of meiotic chromosomes in diploid, triploid and tetraploid *S. tuberosum* was described and analysed. In diploid form, 2 groups of 2 bivalents was frequent, and 6 groups of 2 bivalents was the maximum type. As in the diploid, secondary association was also observed in the triploid. In this form, groups of 3 bivalents were of common occurrence besides groups of 2 bivalents. And at diakinesis and 1st metaphase, trivalents and univalents were observed. Trivalents are, as a rule, either of the triple chain type or Y-shaped with a triple terminal chiasma. In the tetraploid, besides single bivalents, groups of 2 and 3 bivalents were common as in the triploid. In addition to these groups, however, associations of 4 bivalents represented a new distinct class in the tetraploid form. And multivalent associations were not observed.

In potato, aneuploid numbers were first demonstrated by the present author. In 700 cultivated varieties examined, 3 aneuploids having $2n=49$, 47 and 46 chromosomes were found in natural condition. And 20 aneuploids were artificially induced by the hybridization and low temperature treatment. In the former experiment 16 aneuploids, ranging $2n=48$ to 59, were gained. There was no apparent relationship between chromosome number and tuber formation or seed production. In the later experiment, of 75 seedlings which had been subjected to a low temperature of -25°C , an aneuploid having $2n=23$ chromosome constitution was found. It may be induced by a chromosome deficiency.

The subjection of potato plants to low temperature (-10°C for 3-12 hours) has produced various abnormalities on microsporogenesis. Chromatid fragments, fused chromatids and various degrees of asynapsis were occasionally observed in meiosis of PMCs. As the result of asynapsis or suppression of chromosome segregation, diploid pollen grains were often produced. In addition to the above irregularities, low temperature also induced the suppression of cell wall formation.

The sterility and unfruitfulness were examined. The fructification in potato did not take place at the higher air temperature than about 20°C which is an average temperature in day. The degenerations involving both the anther and ovule induced by unfavorable climatic conditions were also demonstrated. Such degenerative change may be mainly due to the shedding of flowers. A male sterile potato was found. This plant was apparently healthy but perfect unfruitfulness, and the mature pollen produced by this plant was nearly normal in amount, but its development was arrested. Pollen abortion induced by the abnormal meiosis, is not the direct cause to explain the potato sterility, although it may be somewhat response for the sterility,

and it is one of factors responsible for it. Some of other factors that influence fruitfulness in potato are restricted habit of bloom, rudimentary to weak inflorescence, ready abscission of flowers, poorly developed stamens and the degeneration of fertile ovules. And most of them appear to be due to the physiological unbalance induced by unfavorable air temperature and environmental conditions, and some one due to genes.

It may be concluded that the original basic number in potato is 6 rather than 12 and that 12 is the secondary origin. This conclusion has been drawn from the following finding: (1) occurrence of secondary association of 6 groups of 2 bivalent chromosomes which was newly demonstrated in diploid form, (2) a peculiar behavior of 6 chromosomes to behave as an individual entity, found in the meiotic division of hybrids from *S. demissum* ($2n=72$) $\times$ *S. tuberosum* ($2n=48$). Then, the genom formulae of diploid set may be written AAAIAI.

Experiments on the inheritance of some characters in potato have been made. Frost and maturity exhibit an incomplete monogenic difference, giving F_2 an approximate ratio of 1:2:1. Yellow of the flesh is a monogenic dominant over white, and the inheritance of tuber color, red $\times$ white, may be explained on a digenic basis. A cross was made between a male sterile plant and a different unrelated male fertile plant. The F_1 plants were self-fruitful, and in F_2 a ratio of 3 fertile:1 sterile was obtained. Male sterility was completely recessive (Table 19). On the other hand, the results obtained from the other cross experiments showed that male sterility was not a simple recessive, namely F_2 plants gave the digenic ratio, 15 fertile:1 sterile (Table 20). These cross results are completely recessive and depend on 2 recessive genes, ms_1 and ms_2 , both of which are necessary for male sterility. This male sterile plant is homozygous, for both these plants contain either one or both of the dominant alleles MS_1 and MS_2 .

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